

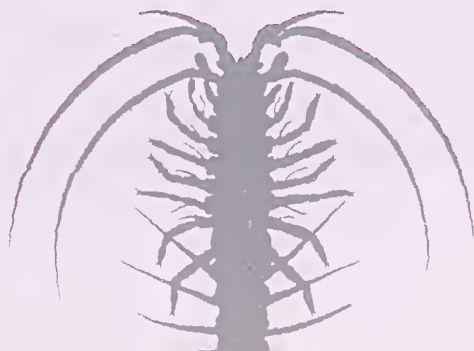
# Evolution of the Biosphere

edited by  
Alexei Yu Rozanov, Patricia Vickers-Rich  
and Chris Tassell



Records of the  
Queen Victoria Museum  
and Art Gallery  
Launceston  
No. 104

1997





© Queen Victoria Museum and Art  
Gallery

Published December 1997

*Records of the Queen Victoria Museum*  
is published by the  
Queen Victoria Museum and Art Gallery,  
Wellington Street,  
Launceston Tasmania 7250  
Australia

Series Editor: Chris Tassell

Editors: Alexei Yu Rozanov  
Patricia Vickers-Rich  
Chris Tassell

Editorial assistance: Kaye Dimmack  
Design: Carolyn Coert  
Printing: Bokprint, 69 Boland Street,  
Launceston.

ISSN 0085 - 5278



# Evolution of the Biosphere

	Introduction .....	5
1.	<b>Biodiversity Dynamics: Indicators of the Biosphere Condition</b> .....	7
1.1	<b>Global Diversity of Proterozoic Stromatolites</b> .....	9
	M. A. Semikhatov and M. E. Raaben	
1.2	<b>Cephalopod Diversity Dynamics in the Silurian</b> .....	15
	I. S. Barskov and G. N. Kisselev	
1.3	<b>Brachiopod and Bryozoan Diversity During Late the Devonian Frasnian–Famennian Extinction Event</b> .....	21
	G. A. Afanasjeva, I. P. Morozova and V. N. Beznosov	
1.4	<b>Diversity Dynamics in the Order Trepostomida (Bryozoa)</b> .....	25
	I. V. Gorjunova, A. V. Markov and E. B. Naimark	
1.5	<b>Changes of the Generic Diversity of Marine Bryozoans (Triassic–Recent)</b> .....	31
	L. A. Viskova	
1.6	<b>Echinoids at the Cretaceous–Paleogene Boundary</b> .....	35
	A. V. Markov and A. N. Solovjev	
1.7	<b>The Quantitative Analysis of Echinoid Evolution</b> .....	39
	A. V. Markov and A. N. Solovjev	
1.8	<b>Biocenotic Preconditions for the Advent of Vertebrates onto Land, and the Position of the Terrestrial Tetrapod Community in the Biosphere of Earth</b> .....	43
	A. S. Rautian	
2.	<b>Crises and Their Symptoms</b> .....	47
2.1	<b>Symptoms of Ecological Crises</b> .....	49
	A. S. Rautian	
2.2	<b>Development of the Late Permian Marine Benthos in a Preecrisis Situation</b> .....	53
	G. A. Afanasjeva and I. P. Morozova	

<b>3.</b>	<b>Ecosystem Reorganization and Biome Formation .....</b>	<b>55</b>
<b>3.1</b>	<b>Phylogenesis and Phylocenogenesis .....</b>	<b>57</b>
	V. V. Zherikhin	
<b>3.2</b>	<b>Succession Pruning: a Possible Mechanism of Biome Diversification .....</b>	<b>65</b>
	V. V. Zherikhin	
<b>3.3</b>	<b>Density, Diversity and a General Model of Ecosystem Evolution .....</b>	<b>75</b>
	V. A. Krassilov	
<b>4.</b>	<b>Evolution of Biochores in the Phanerozoic .....</b>	<b>81</b>
<b>4.1</b>	<b>Some Aspects of Global Paleobiogeography in the Phanerozoic .....</b>	<b>83</b>
	T. A. Grunt and A. Yu. Rozanov	
<b>4.2</b>	<b>Biogeographic Zonation of the Late Eocene–Early Miocene Tethys–Paratethys Basins based on Bivalve Data .....</b>	<b>89</b>
	S. V. Popov	
<b>4.3</b>	<b>Historical Zoogeography of Terrestrial Tetrapods: A New Method of Global Palaeogeographical Reconstructions .....</b>	<b>95</b>
	N. N. Kalandadze and A. S. Rautian	
<b>4.4</b>	<b>Biogeography and Evolution of Faunistic Complexes .....</b>	<b>99</b>
	E. B. Naimark and A. V. Markov	

## Introduction

For the last five years in Russia research has been carried out under a Russian Governmental Programme called 'Global Changes of the Environment and Climate'. A part of this programme has been the setting up of a working group on the evolution of the biosphere through time so that comparison could be made to change caused by humans alone. This comparison then gives the opportunity to develop a strategy that could be followed to save the biosphere and soften the anthropogenic crisis in which we now find ourselves.

A number of researchers took part in this programme, many from the Palaeontological Institute, the Geological Institute, the Institute of Lithosphere, and the Institute of Geology and Geophysics in Russia. All belong to the Russian Academy of Science. Moscow State University and VSEGEI personnel also participated.

Every year special meetings were held to discuss the results of the investigations under this programme — about 130–150 reports resulted from each of these meetings.

The historical perspective of the palaeontological and geological data gives a real chance to evaluate the present-day condition of the biosphere and to then define our strategy for future behaviour.

Several objectives were outlined at the beginning of this programme:

1. creation of a data bank of past biodiversity;
2. study the dynamics of diversity through time;
3. plot the biogeographic distributions and look at the dynamics of biogeographical changes through time;
4. pose a number of questions about the nature of the biotic crises and their sequence of events. It is known that in the history of the Earth there were several of these crises that had a whole set of different consequences.

Researchers have suggested that the biosphere has been a self-controlled, self-regulating system. Analysis of these past crises in this biosphere programme has given us insights into whether this indeed has been the case.

It is clear that anthropogenic influence eventually evokes a reaction from the biosphere. Some influences are wrought by those that put no thought into the consequences, only looking at the short-term gain. Such activities could eventually destroy man as a biological species, by preventing the biosphere from functioning normally. We hope that the insights from these papers that deal with past changes and crises in the biosphere over the last 4 billion years may give some insights about future directions.

Three previous volumes devoted to papers produced in this programme have been published in Russian. The current authors in this volume bring some of the previous results from other volumes, in English, to a wider circle of readers. That is why the Queen Victoria Museum and Art Gallery and the Monash Science Centre agreed to publish this collection.

It should be mentioned that work on this project gave rise to a whole series of new ideas and new directions of research. One of these directions is conditionally called 'Bacteriological Palaeontology'. Not long ago it was difficult to imagine that we could recognize fossil bacteriological communities. Now, with the aid of scanning electronic microscopy and other methods we can study cyanobacterial and associated microscopic communities in most sedimentary sequences.

The ability to publish this volume was the result of a cooperative effort between the Palaeontological Institute of the Russian Academy of Science, the Monash Science Centre and the Queen Victoria Museum and Art Gallery who worked together to set up and tour *The Great Russian Dinosaurs* Exhibition from 1993 until 1997. The proceeds from that exhibition has helped more than 150 scientists and technicians from Russia, Australia and the United States to undertake cooperative projects and has funded the publication of these papers. This has been truly a cooperative venture. In the words of Valentin Krassilov, one of the authors in this volume: 'It is due to creative, rather than competitive, species and people that progress occurs in both biological and social systems'. It has certainly been that very cooperation which has nurtured the production of this set of papers originally presented at a number of symposia and this volume of thoughts and new ideas.

Alexei Rozanov  
Moscow  
April 1997



**Biodiversity  
Dynamics:  
Indicators of the  
Biosphere Condition**

**1**







## 1.1 Global Diversity of Proterozoic Stromatolites

M. A. Semikhatov and M. E. Raaben

### Abstract

The dynamics of global diversity of Proterozoic stromatolites is analysed at specific and generic levels on the basis of separate records from each of six superregions: northern Eurasia, China, India, Africa, Australia, and North America. The analysis involves eleven time units of comparable duration. Four units are delimited in the Early Proterozoic and seven in the Late Proterozoic (Riphean and Vendian). The secular changes in the Proterozoic stromatolite diversity are considered against the background of abiotic and biotic events and this reflects directed evolution of Proterozoic ecosystems.

Stromatolites are an important source of biogeological information concerning the long interval of the Precambrian preceding to the Vendian diversification of Metazoa. Stromatolites were rare in the Archaean, but the Proterozoic was the time of their maximum abundance, taxonomic diversity and ecological expansion for the whole geological record. Being organosedimentary structures, stromatolite buildups reflect in their diagnostic features a complicated interaction between microbial communities and the surrounding environments. Although the mechanism of this reflection is not thoroughly understood, stromatolite microstructure, the main or single criterion for delimitation of the formal species (forms), is related to the taxonomic composition of the stromatolite-forming communities (see Semikhatov & Raaben 1993, 1996 for bibliography).

Understanding the biogeological informativeness of stromatolites, many researchers, beginning with Maslov (1959), attempted to evaluate their secular variations in diversity and abundance first on a qualitative (see Semikhatov & Raaben 1993, for bibliography), and then on a quantitative basis (Awramik 1971, 1991, 1992; Walter & Heys 1985; Cao 1988; Semikhatov & Raaben 1993, 1994, 1996). At present, diversity increased from the Archaean to the Late Proterozoic, reached a maximum in some interval of the Late Riphean, and then rapidly decreased at the end of the Precambrian and in the Cambrian, thus reflecting a general decline of the stromatolites in Phanerozoic times.

In order to explore the diversity dynamics of the Proterozoic stromatolites, authors of this paper (Semikhatov & Raaben 1994, 1996) have analysed them at both specific and generic levels. Another part of our analysis concerns stromatolite diversity dynamics across six extensive regions, namely northern Eurasia, China, India, Africa, Australia and North America, preceded by the analysis of the global diversity, which was based on summarised regional samples of taxa. Such an approach made it possible to minimise the statistical noise related to the nonuniform concept of taxa by different researchers and to better understand the correlations between stromatolite diversity variations and geological events.

The stratigraphic framework used in our analysis is the refined stratigraphic scale adopted for the Precambrian of northern Eurasia within the borders of the former USSR (Semikhatov et al. 1991). For our purposes, four informal units were delimited within the Lower Proterozoic (Karelian) of that scale ( $2500 \pm 50 - 1650 \pm 50$  Ma), which virtually coincides with the Paleoproterozoic of the geological time-scale proposed by the International Subcommission on Precambrian Stratigraphy (Plumb 1991). These units, with lower boundaries dated at 2300, 2000, 1800 Ma, are equal or similar in their time range to the Paleoproterozoic units of the International Subcommission scale. The Riphean–Vendian interval (Mezo- and Neoproterozoic) in our scale was subdivided into seven units: two in each of the three Riphean erathems plus the Vendian system. The isotopic ages of the lower boundaries of the above erathems — of the Lower, Middle and Upper Riphean (the Burzyanian, Yurmatinian and Karatavian) — are known to be  $1650 \pm 50$ ,  $1350 \pm 20$  and  $1000 \pm 50$  Ma, while the boundaries between the above subordinate units are dated at 1450, 1200 and 860 Ma.

The age of the base of the rock sequence in the Vendian, contrary to the opinion of some geologists (e.g. Harland et al. 1990; Knoll & Walter 1992), is considered to be  $650 \pm 20$  Ma according to data obtained for the Laplandian (Varangerian), Glaciohorizon proper (Keller & Semikhatov 1990; Semikhatov et al. 1991), since the base of that unit, by definition, determines the Vendian lower boundary.

Calculating the frequency of occurrence of stromatolite taxa, we have taken into account, in addition to the published data, some original material: the results of our study of the type collections described by Ch. Walcott, C. Fenton, M. Fenton, R. Rezak, S. Knight, and J. Bertrand-Sarfati as well as the identifications of material collected by one of us (MAS) in North American sections. The samples of taxa of formal species rank include those species and varieties described in the literature, which we considered valid, and those stromatolites identified in publications at the generic level only or in the open nomenclature if they are either the only representative of a group in the relevant time-unit or have a specific

microstructure. The formal species cited in literature with any uncertainty were not taken into account in our calculations.

It seems that the diversity dynamics of the Proterozoic stromatolites followed the same trends at the specific (Semikhatov & Raaben 1993, 1994, 1996) and generic levels in each of the six regions under analysis, and all of the regional diversity histograms, in spite of some peculiarities, demonstrate important common features. Their similarity is striking during the Early and Late Proterozoic intervals. A majority of the regional histograms demonstrates a trimodal pattern of higher stromatolite taxonomic diversity in the course of the Proterozoic, and its subsequent significant decrease at the end of the Riphean. Diversity maxima occur at the following intervals:

1. 2.3–2.0 (northern Eurasia, China, India) or 2.0–1.8 Ga ago (Australia);
2. 1.65–1.45 Ga ago, in the Early Burzyanian (northern Eurasia, China, India, Australia);
3. 1.0–0.85 Ga ago, in the Early Karatavian (northern Eurasia, China), or 0.85–0.65 Ga ago, in the Late Karatavian (Australia), or 1.0–0.65 Ga ago, in the entire Late Riphean (India).

Exceptions are the American and African histograms, which are of a bimodal character. The first of them is devoid of the Early Burzyanian peak and the second — of the Early Proterozoic one. However, due to the position of two other maxima, the American and African histograms are very similar to those of Australian and north Eurasian graphs, respectively. The revealed similarity between the regional histograms suggests that each of them reflects important events of wide significance.

Figure 1 presents the results of summation of all regional samples representing continents with reasonably adequate identifications of Proterozoic stromatolites. In essence, this graphs global stromatolite diversity. It reflects secular distribution of 236 formal genera and 908 species. The latter value is only slightly distinct from the sum of all relevant taxa in the regional samples. That is due to a low percentage (c. 8.5%) of species recorded to cross the boundary of a single superregion. The corresponding value for genera is much higher (c. 31%). The low percentage of species in common between two or several regions depends on the high degree of the endemism of Proterozoic stromatolite assemblages (Semikhatov 1985) and, to some extent, probably on the presence of yet undetected synonyms in the samples.

The histograms in figure 1 summarise global diversity dynamics of Proterozoic stromatolites at the specific and generic levels. The main features of both histograms are as follows:

1. The trimodal shape with the peak location at the middle part of the Early Proterozoic (2.3–2.0 Ga),

Early Burzyanian (1.65–1.45 Ga), and Early Karatavian (1.0–0.85 Ga);

2. Minima of taxonomic diversity at the beginning (2.5–2.3 Ga) and very end (1.8–1.65 Ga) of the Early Proterozoic;
3. A sharp decrease in the number of taxa in the Late Burzyanian (1.45–1.35 Ga) and a gradual rise of diversity during the Yurmatinian (Middle Riphean);
4. A considerable diversity decline in the Late Karatavian (0.85–0.65 Ga), which continued into the Vendian.

Literally interpreted, the available data implies continuation of this decrease into the Cambrian. However this conclusion seems tenuous due to insufficient information on the taxonomy of the Cambrian stromatolites, at present.

The global histograms of generic and specific diversity are similar in their main features, but each has some peculiarities. For instance, the species histogram indicates an Early Karatavian peak that is 1.7 times higher than the two other peaks and a very wide amplitude of variations. The generic histogram shows less contrast; the Early Karatavian peak is not so prominent, while the Early Proterozoic peak (2.3–2.0 Ga) is unexpectedly large. This seems to have resulted from the interaction of three different factors:

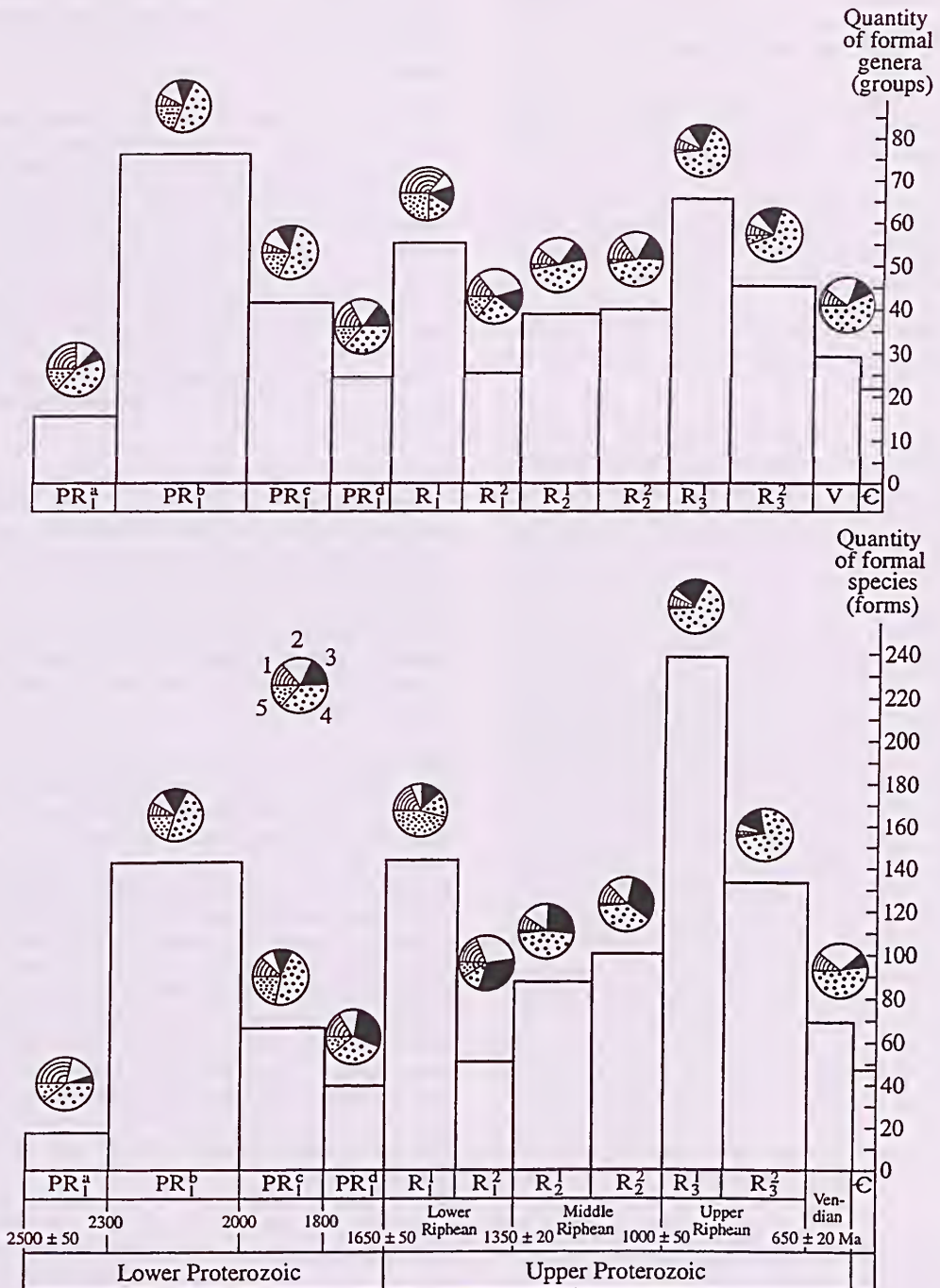
1. An increase of the average number of species per genus during the Proterozoic;
2. The higher degree of endemism of the Early Proterozoic stromatolite assemblages in comparison with those of the Riphean and Vendian ones (Semikhatov 1985);
3. The apparent oversplitting of the Early Proterozoic stromatolite formal genera in China, especially their branching forms that dominate the maximum in question.

Thus, the available data do not provide the unambiguous conclusion that the generic (=morphological) stromatolite diversity was at its maximum 2.3–2.0 Ga ago. However, these data demonstrate that stromatolite species in the modern classifications, were most diverse in the Early Karatavian and afterwards declined.

Secular variations in the inner structure of the Proterozoic stromatolite assemblages (redistribution of the relative abundance of the supergeneric categories) are shown in the circular diagrams of figure 1. These diagrams demonstrate that:

- (a) The percentage of columnar branching stromatolite taxa increased twice — from the beginning of the





**Figure 1** Secular variations in global diversity of Proterozoic stromatolites at the level of formal species (form) and formal genera (groups) and secular structural changes in their assemblages (after Semikhatov & Raaben 1996).

(1-5), percentage of species and genera in the following supergeneric categories of stromatolites:

1. Stratiform
2. Nodular
3. Columnar unbranching
4. Columnar branching
5. Microstromatolites

Proterozoic until 2.0–1.8 Ga and from the Middle Riphean until the Late Karatavian and declined 1.8–1.35 Ga ago and in the Vendian time;

- (b) The Riphean taxa of stratiform and nodular stromatolites exhibit secular variations in relative abundance in contrast to those of the columnar forms;
- (c) The diversity of microstromatolites (*Asperia*-form buildups) increased from the beginning of the Proterozoic until the Early Burzyanian and sharply declined in the younger geologic record.

As a result, each of the maxima and minima of the global histograms has its own unique ratio of taxa belonging to different supergeneric categories.

The changes in taxonomic diversity of Proterozoic stromatolites was controlled by many factors with a complex feedback system (see Semikhatov & Raaben 1996 for detailed discussion). The dominant factor influencing diversity (and abundance) was tectonics, both long-term and short-term trends. Basic elements that allowed stromatolite development first occurred in the Late Archean, but the extensive formation of vast carbonate platforms took place only in the Early and increased in the Late Proterozoic, after the appearance of the epi-Archean and much larger epi-Svecofennian (epi-Hudsonian) cratons were covered by shallow epicratonic seas. However, the appearance of large, stable continental masses does not mean *a priori* high stromatolite diversity and abundance. Short-term tectonic events were needed to trigger the diversity peak 2.3–2.0 Ga ago, as is evident from geological records in Karelia, Scandinavia and China. The sharp decrease in the global stromatolite diversity about 2.0 Ga ago can be attributed to both the Lulang Orogeny in mobile belts of China, and the reduction of carbonate accumulation in the Baltic Shield. The marked drop in diversity and abundance of stromatolites at the very end of the Early Proterozoic (1.8–1.65 Ga ago) was evidently related to the Svecofennian, Hudsonian, and Burramundian orogenies, which almost simultaneously (1.92–1.8 Ga ago) affected vast areas of shallow water environments and caused elevation of several cratons, wide distribution of elastic and volcanoclastic sedimentary complexes and sharp reduction of carbonate accumulation.

The Early Burzyanian diversity peak correlates with extensive marine transgressions onto continents and origination of some mobile belts (e.g. Kibaran) with a noticeable increase in carbonate sedimentation. The increase in stromatolites diversity from the Early Yurmatinian to the Early Karatavian occurred against the background of a progressive subsidence of the stable massifs with corresponding expansion of epicontinental seas (e.g. Africa, Eastern China, Central Siberia), and the formation of a series of intracratonic mobile belts, the largest of which appeared c. 1.0 Ga ago in Africa. However, chronological coincidence of the Early

Karatavian increase in diversity with other important biospheric events strongly suggest that the above tectonic events were hardly the sole, or even the main, cause of the increase.

The Late Karatavian drop in stromatolite diversity seems to be directly related to the emergence of extensive stable massifs in Eurasia and almost synchronous (850–800 Ma) with the Early Baikalian, Jinning and Lusakan orogenies, which led to extinction of several mobile belts and wide distribution of siliciclastic sediments in China, Siberia and Africa. The subsequent Vendian decrease in diversity occurred against the background of contrasting tectonic events — the Pan-African orogeny and post-glacial marine transgression, which produced massive shallow water carbonates (e.g. South China, Siberia), were favourable for stromatolite development, although deficient in them.

Correlation between the Late Riphean–Vendian stromatolite diversity and geodynamics can be inferred from the analysis of secular variation of  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio in sea water. This ratio reflects the relationships between continental runoff and mantle influx in the World Ocean (see Gorokhov et al. 1995 for original data and review). The Early Karatavian peak and Late Karatavian–Vendian decrease in diversity were coeval with important changes in the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio (its considerable drop and rapid increase, respectively).

At the same time, recent models of Precambrian sea water chemical evolution opens the possibility of relating some features of stromatolite diversity to major trends in the carbonate accumulation during the Proterozoic time (Grotzinger 1990; Sochava & Podkovyrov 1993; Semikhatov & Raaben 1993, 1996). It is important to note that microstromatolites, which are regarded now, completely or partly, as precipitates (e.g. Grotzinger 1990), played an important role in the pre-Late Burzyanian stromatolite assemblages and disappeared from the geological record almost completely during the Middle Riphean. The most diverse Early Karatavian stromatolite set is confined to the carbonates which demonstrate specific lithological, mineralogical and chemical features as compared with their pre-Karatavian and Vendian counterparts (see Semikhatov & Raaben 1996 for bibliography).

Correlation between the major pre-Vendian palaeoclimatic changes and stromatolite diversity seems obvious. Termination of the Early Palaeoproterozoic (Canadian) *Glacioera* and the climate aridification were most likely among the factors that induced the first diversity peak (2.3–2.0 Ga). The Late Karatavian decrease in diversity occurred during the time range of the African *Glacioera* (Chumakov 1992), which affected the main parameters of carbonate sedimentation. The Vendian decrease in diversity occurred after the Laplandian (Varangerian) glaciation against the background of palaeogeographic (see above) and palaeoenvironmental



changes (Brasier 1992; Sochava & Podkovyrov 1993), which produced favourable prerequisites for the increase in stromatolite development and diversity. The evident contradiction between these prerequisites and the real data show a powerful factor influencing stromatolite formation emerged during the Vendian.

The relation between stromatolite diversity and some biological events can be highlighted by analysing variations in the carbonate/carbon isotopic composition. Close association of the largest positive  $\delta^{13}\text{C}$  shift during the Proterozoic (e.g. Karhu 1993) with the Early Proterozoic diversity peak, primarily defined by taxa from the 2.2–2.1 Ga-old successions (Semikhatov & Raaben 1994, 1996), strongly suggest that this peak in diversity was related to the radical increase of bioproductivity of photosynthetic organisms and Corg. burial — a phenomenon which is of global importance. In contrast, late Paleoproterozoic–Middle Riphean changes in stromatolite diversity (including Early Burzyanian peak) occurred against a background of relatively stable  $\delta^{13}\text{C}$  values in carbonates. The Early Karatavian diversity peak, is located near the beginning of a distinct rise in  $\delta^{13}\text{C}$  in carbonates (e.g. Knoll et al. 1995).

Such correlation is in concert with both proliferation of stromatolites (i.e. stromatolite-forming microbial communities) 1.0–0.85 Ga ago and significant evolutionary innovations in the microbiota microbes at the Middle–Late Riphean transition (Knoll 1994; Knoll & Sergeev 1995). These events were very likely to affect bioproductivity in the oceans and the rate of Corg. burial, although the latter phenomenon could be enhanced as well by lowered oxidation potential of the Early Karatavian sea water, deduced from  $^{87}\text{Sr}/^{86}\text{Sr}$  (Gorokhov et al. 1995). It seems surprising that the Late Karatavian and Vendian stromatolite decline coincides with very noticeable general increase of  $\delta^{13}\text{C}$  values in carbonates. In this respect, it is important that Late Riphean and Vendian time was marked by expansion of global distribution of marine algae (seaweed) and other lower eucaryotes (Knoll & Walter 1992; Knoll 1994), which may have competitively excluded cyanobacteria as the main producer of biomass in marine environments.

Understanding the relationship of stromatolite diversity and changes in the taxonomic composition of the Proterozoic microbiota is obviously hampered by:

- (a) Extreme evolutionary (morphological) conservatism of stromatolite-forming cyanobacteria;
- (b) Uncertain relations between taxonomic composition of mat-forming microbial communities and stromatolite microstructure; and
- (c) Diagenetic and epigenetic alternation of the latter.

However, profound changes in microbial taxonomic composition at the Middle–Late Riphean (Mezo- and

Neoproterozoic) transition and diversification and expansion of seaweeds about 900–850 Ma ago (Knoll 1994; Knoll & Sergeev 1995) seem to correlate with the Early Karatavian rise and Late Karatavian reduction of stromatolite diversity, respectively. Appearance of diverse eucaryotes and new groups and size classes of procaryotes in the Early Karatavian benthic microbial communities might have expanded the adaptive abilities of the latter and given rise to diversity of stromatolites proper and their microstructures. On the contrary, the Late Karatavian expansion of seaweeds might have resulted in reduction of cyanobacterial mat distribution and a related decline of stromatolites (see Semikhatov & Raaben 1993, 1996 for detailed discussion and bibliography). This decline was most likely promoted by several abiotic factors, partly related to the onset of the African *Glacioera*. The Vendian decrease in the stromatolite diversity is usually attributed to the appearance of burrowing and grazing metazoans in benthic ecosystems and restructure of cyanobacterial mats to environments unfavourable to metazoans (e.g. Awramik 1971, 1991, 1992; Walter & Heys 1985; Semikhatov & Raaben 1993, 1996).

Thus, the taxonomic diversity of Proterozoic stromatolites has depended on a complex of interrelated and independent abiotic and biotic factors, the general evolution of Proterozoic ecosystems. The course of events, with regard to stromatolites, were by the Early Proterozoic and Early Karatavian diversity peaks as well as by late Paleoproterozoic, Late Karatavian, and Vendian decreases in stromatolite diversity. Peaks of stromatolite diversity (as well as abundance), related to periods of proliferation of mat-forming microbial communities, were, by themselves, important biospheric events which caused the burial of great masses of  $\text{CO}_2$  in carbonate sediments and directly affected global environments.

The authors would like to thank S. M. Awramik, M. A. Fedonkin, K. Grey, A. H. Knoll, W. V. Preiss, and M. R. Walter for fruitful discussions of the problems considered in this paper. This work was supported by the Russian Foundation for Basic Research, Project No. 96-05-64329.

## References

- Awramik, S. M. 1971, 'Precambrian columnar stromatolite diversity: Reflection of metazoan appearance', *Science*, vol. 174, pp. 825–827.
- Awramik, S. M. 1991, 'Archean and Proterozoic stromatolites', in *Calcareous Algae and stromatolites in Early Organic Evolution: Implications for Mineral and Energy Resources*, ed. M. Schidlowski, Springer-Verlag, Berlin pp. 289–304.
- Awramik, S. M. 1992, 'The history and significance of stromatolites', in *Early Organic Evolution: Implications for Mineral and Energy Resources*, ed. M. Schidlowski, Springer-Verlag, Berlin, pp. 435–449.
- Brasier, M. D. 1992, 'Global ocean-atmosphere change across the Precambrian-Cambrian transition', *Geol. Mag.*, vol. 129 no. 2, pp. 161–168.
- Cao, R. 1988, 'Study of stromatolite decline event in terminal Precambrian', *Acta Palaeontol. Sinica*, vol. 27 no. 6, pp. 837–852.

- Chumakov, N. M. 1992, 'The Problems of old glaciations (pre-Pleistocene glaciogeology in the USSR)', *Soviet Sci. Reviews, Section G. Geology Reviews*, vol. 1 no. 3, 208 pp.
- Gorokhov, I. M., Semikhatov, M. A., Baskakov, A. V., et al. 1995, 'Stratigraphic composition in the Riphean, Vendian and Lower Cambrian carbonates from Siberia', *Strat. and Geol. Correlation*, vol. 3 no. 1, pp. 1–28.
- Grotzinger, J. P. 1990, 'Geochemical model for Proterozoic stromatolite decline', *Am. Jour. Sci.*, vol. 290-A, pp. 80–103.
- Harland, B. W., Armstrong, R. L., Cox, A. V., et al. 1990, *A Geological Time-Scale*, Cambridge Univ. Press, Cambridge, 263 pp.
- Karhu, J. A. 1993, 'Paleoproterozoic evolution of the carbon isotope ratios of sedimentary carbonates in the Fennoscandian Shield', *Bull. Geol. Surv. Fin.*, vol. 371, pp. 1–96.
- Keller, B. M., & Semikhatov, M. A. 1990, 'Isotope Geochronology for the Vendian of the USSR', in *The Vendian System 2, Regional Geology*, eds B. S. Sokolov and M. A. Fedonkin, Springer-Verlag, Berlin, pp. 184–190.
- Knoll, A. H. 1994, 'Proterozoic and Early Cambrian Protists: Evidence for accelerating evolution' *Tempo. Proc. Nat. Acad. Sci. U.S.A.*, vol. 91 no. 15, pp. 6743–6750.
- Knoll, A. H., & Sergeev, V. N. 1995, 'Taphonomic and evolutionary changes across the Mesoproterozoic-Neoproterozoic transition', *N.Jb. Geol. Paleont., Abh.* 195 (1-3), pp. 289–302.
- Knoll, A. H., & Walter, M. R. 1992, 'Latest Proterozoic stratigraphy and earth history', *Nature*, vol. 356, pp. 675–678.
- Knoll, A. H., Kaufman, A. J., & M Semikhatov, M. A. 1995, 'The carbon isotope composition of Proterozoic carbonates: Riphean succession from northern Siberia (Anabar Massif, Turukhansk Uplift)', *Geol. Mag.*, vol. 295 no. 7, pp. 823–850.
- Maslov, V. P. 1959, 'Stromatolites and facies', *Dok. Akad. Nauk SSSR*, vol. 125 no. 5, pp. 1085–1088.
- Plumb, K. A. 1991, 'New Precambrian time scale', *Episodes*, vol. 14 no. 2, pp. 139–140.
- Semikhatov, M. A. 1985, 'Stromatolites and Precambrian stratigraphy: an analysis '84', *Izv. Akad. Nauk SSSR, Ser. Geol.*, no. 4, pp. 3–21.
- Semikhatov, M. A., & Raaben, M. E. 1993, 'Dynamics of the taxonomic diversity of Riphean and Vendian stromatolites in northern Eurasia', *Strat. Geol. Correlation*, vol. 1 no. 2, pp. 133–141.
- Semikhatov, M. A., & Raaben, M. E. 1994, 'Dynamics of the global diversity of Proterozoic stromatolites. Article 1: Northern Eurasia, China and India', *Strat. Geol. Correlation*, vol. 2 no. 6, pp. 492–513.
- Semikhatov, M. A. & Raaben, M. E. 1996, 'Dynamics of the global diversity of Proterozoic stromatolites. Article 2: Africa, Australia, North America, and General Synthesis', *Strat. Geol. Correlation*, vol. 4 no. 1, pp. 24–50.
- Semikhatov, M. A., Shurkin, K. A., Aksenov, E. M., et al. 1991, 'A New Precambrian stratigraphic scale of the Soviet Union', *Izv. Akad. Nauk SSSR, Ser. Geol.* no. 4, pp. 3–13.
- Sochava, A. V. & Podkovyrov, V. N. 1993, 'Evolution of the composition of carbonate rocks in the late Precambrian', *Strat. Geol. Correlation*, vol. 1 no. 4, pp. 378–392.
- Walter, M. R., & Heys, G. R. 1985, 'Links between the rise of the Metazoa and the decline of Stromatolites', *Precamb. Res.*, vol. 29 no. 1, pp. 149–174.



## 1.2 Cephalopod Diversity Dynamics in the Silurian

I. S. Barskov and G. N. Kisselev

### Introduction

Cephalopods are one of the most important components of the Silurian marine biota. The recent generic revision of the world date at the stage/time level made within the framework of the government science program, 'Changes of natural environment and climates', shows the extraordinary high diversity of the Silurian non-ammonoid cephalopods. In the Wenlockian, the cephalopod diversity maximum exceeds diversity in any other period of the history of this group, and it reaches an absolute maximum in the Fammenian (ammonoids and non-ammonoid cephalopod (Barskov et al. 1994)). An obvious next step in studies on this group must be more detailed research: analysis of the development of cephalopod communities in the separate biogeographic regions. These studies could not be made before, but in this past decade our knowledge of the Silurian cephalopods from many different regions of the former USSR have increased, and now is adequate for regional comparisons.

### Previous Work

The several schemes of the generic diversity in the Silurian stages have been published recently (Barskov et al. 1994; Kisselev 1992). In spite of some local differences the general global trends are the same as those viewed in the USSR. Generic and species diversity declines after the Late Ordovician mass extinction event, increases to a maximum in the Middle Silurian and decreases gradually by the beginning of the Devonian and reaches a low point in the Early Devonian. Some of the peculiarities of cephalopod assemblages in different regions have been discussed by Kisselev (1989, 1992).

### Material

The data from published recent monographs and revisions (Siberian Platform – Bogolepova 1989, Balashov 1962, Mjagkova 1967; North of the Urals – Kisselev 1982; Baltic region – Kisselev 1989a, 1989b, 1990; Podolia – Kisselev 1989b; Southern Tian Shan – Barskov et al. 1994, Kisselev 1993a, 1993b; Kazakhstan – Barskov 1972) and some authors' unpublished materials were used in the studies discussed in this paper.

### Results and Discussion

The generally accepted biogeographic subdivisions for the Silurian are not totally agreed upon by all researchers in this area. Boucot (1975) established the only Silurian realm with a provisional two or three provinces. Each of the regions discussed in this paper could be considered as a separate biogeographic province. More than 60% of species and 50% of the genera in them are endemic to the

region. We propose that the only realistic criterion to combine the regions in the more extensive biochories should be the summarised domination of the genera and species belonging to higher taxa (orders), but not the number of endemic forms. This criterion has been successfully used in the biogeographic comparison of the Ordovician cephalopod biotas (Barskov 1972).

Eurysiphonate actinoceroids prevail over other taxa in the Middle Ordovician of the Siberian Basin, both taxonomically and quantitatively. Endoceroids and coiled tarphycerids dominate in Baltic faunas. In Kazakhstan, endoceroids and actinoceroids are absent, but there are a number of cyrtoconic oncocerids and discosorids. Kazakhstan Ordovician faunas are more similar to those of the North American Appalachians than to Baltic or Siberian faunas, in spite of some common genera and species. There are endoceroids and tarphycerids in the Middle–Late Ordovician faunas of Southern Tian Shan, and these can well be compared with Baltic cephalopod communities. Based on Ordovician climatic reconstructions, we consider the Siberian faunas (and very similar North American mid-continent ones) as warmer-water, Kazakhstan (and Northern American Appalachian ones) as cold-water and Baltic ones as temperate.

Distribution of the main cephalopod orders in the first half of the Silurian, in spite of evolutionary changes in the generic groups, is very similar to Ordovician distribution. Endoceroids and ellesmerocerids, for example, were extinct by the end of the Ordovician, the diversity of ortoceroids increased and the diversity of tarphycerids, to the contrary decreased. Generic composition of oncocerids and discosorids changed. Such changes differ in the different regions.

### Siberian Basin

At least twenty cephalopod species have been reported from the Ashgillian by now. The number of eurysiphonate actinoceroids has decreased in comparison to those known from Middle Ordovician assemblages of this region; a few endoceroid and tarphycerid species appear at the end of the Ashgillian. The taxonomic structure of the cephalopod community is similar to the Middle Ordovician Baltic assemblages. These changes apparently reflect the cooler global climate in Ashgillian times when temperate genera migrate into a more tropical zone. More than thirty species in twenty-seven genera exist in the Llandoveryan in the Siberian Basin. Five or six species of these belong to eurysiphonate actinoceroids. The appearance of these taxa demonstrates that the temperatures became warmer in the Llandoveryan Ashgillian. Thirteen species in thirteen genera are known from the Wenlockian; one-third of these are

euryisiphonate actinoceroids. This faunal mix, the fact that each genus is represented by one single species supports the idea that the climate was warming into the Wenlockian. The appearance of coral-stromatoporoid biostromal masses further confirms this conclusion (Bogolepova 1989). In the Ludlowian cephalopod diversity decreases, perhaps related to the lagoonal nature of the faunas, deposited in dolomites, gypsum; stromatolites appear in the Ludlowian deposits. Bogolepova (1989) described six species. The same number of undescribed forms are contained in the author's collection. There is no marine sedimentation during the Late Ludlowian and Pridolian ages.

The cephalopod distribution in the Silurian of the Siberian Basin have two main characters:

1. The Llandoveryan diversity is higher than the Ashgillian. That means the changes seem opposite to global changes (Barskov et al. 1994);
2. The Wenlockian diversity maximum presented in the global generic diversity curve is not observed in this region.

### Baltic Region

Cephalopod development and the diversity dynamics at the end of the Ordovician and in the Silurian are quite different. About fifteen species are known from the Ashgillian. Orthoceroids predominate. Endoceroids were widely distributed in the Middle Ordovician in this region and are represented by only two species. This might be evidence of the relative cooling of climate. The Llandoveryan cephalopod fauna is very poor (six or seven species) and half of them are euryisiphonate actinoceroids. They are considered to be indicators of relatively warm climate. There are no oncocerids and discosorids. The data on the Wenlockian cephalopods are contradictory. More than 100 species have been mentioned in some previous publications (Kisselev 1989a, 1989b, 1990), but this information is dubious, and revision is necessary. Twenty species are known for sure (Kisselev 1989a, 1990). The real diversity must be higher, but at present, it is more important to conclude that the cephalopod diversity maximum falls in the Wenlockian for this region. The Ludlowian cephalopod diversity decreases to fifteen species and is a bit higher in the Pridolian. The increasing of the proportion of the cyrtoconic oncocerids to the Middle Silurian and predominance of orthoceroids at the end of the Silurian is the general change in the taxonomic structure. On the whole, the diversity dynamics of the Silurian cephalopod community in the Baltic region corresponds well to the global changes known for this time.

### Southern Tian Shan

The diversity dynamics in the Silurian of this region show another change. More than eighteen undescribed species

are known from the Ashgillian. There are endoceroids and coiled tarphycerids. Thus, the cephalopod taxonomic structure is very similar to that of the Middle Ordovician of Baltic and Scandinavian assemblages. The Southern Tian Shan region belongs to the intermediate temperate climatic zone. In the Llandoveryan the diversity increases and cyrtoconic oncocerids and discosorids predominate (about 70% of the cephalopod diversity). This feature is a distinct characteristic of the region. The following diversity dynamics are also special. In the Wenlockian, the general number of species decreases and orthoconic orthoceroids take on a greater importance. Actinoceroids are represented by the genus *Eushantungoceras* known in the Wenlockian from Baltic, Northern Urals, Barrandien, Podolia. The Ludlowian cephalopod assemblages are characterised by unprecedented increase in diversity (more than fifty species of about thirty genera). Oncocerids and discosorids predominate in the Ludlowian, forming more than 60% of the cephalopod fauna. The Pridolian diversity remains high, but the taxonomic structure of the community changes: about 60% is orthoconic orthocerids and pseudorthocerids.

### Northern Urals

The Late Ordovician cephalopods from this region are not known, and the only orthoceroid species have been described from the Llandoveryan. Eleven species have been described from the Wenlockian (Kisselev 1982). Five belong to one genus, *Phragmoceras* (cyrtoconic discosorids), which was known before from the Silurian of Gotland, and two species are oncocerids. As in the Tian Shan region, the Ludlowian cephalopod diversity increases (more than fifty species), oncocerids dominate. In this respect the Urals, Tian Shan and Kazakhstan (see below) are much more similar to each other than to any other regions. The Pridolian cephalopod diversity is twenty to twenty-five species, of which the orthocerids predominate.

The Silurian cephalopod biotas of the four above-mentioned regions are distinct. In other areas cephalopod assemblages are not as diverse. The reason for this could be either their primary 'poorness', unfavourable living conditions (Podolia as the example) or poorer preservation potential (the terrigenous deposits in Central Kazakhstan) or unsatisfactory description and publication (Tuva). Nevertheless, it is important to take them into consideration.

### Podolia

About a dozen species are known from the Late Ordovician of this region (Molodovsky Horizon). Only one undoubted species has been described from the Llandoveryan. Fifteen species are presented in the Wenlockian and orthocerids predominate. The increasing diversity in the Ludlowian (about twenty species) is characterised by the equal ratios of orthoceroids and



oncoceroids. There are also actinoceroids and tarphycerids. In the Pridolian the diversity falls, the taxonomic structure remains similar.

### Central Kazakhstan

The Late Ordovician cephalopods of Kazakhstan are numerous (twenty-four described species in sixteen genera) and diverse. The majority are oncocerids and discosorids. In this respect, as it has been already discussed by Barskov (1972), these assemblages are more similar to cephalopod assemblages of the Appalachian region of the USA than to the Baltic or Siberian assemblages. Four species have been described from the Llandoveryan and ten from Wenlockian, but the data are not complete. In the Wenlockian, the number of oncoceroids exceeds the orthoceroids. This phenomenon is most unusual for the other regions. A decrease in the number of species in the Ludlowian and an increase in the Pridolian corresponds to the changes of the taxonomic structure towards predominance of orthoceroids.

### Tuva

The cephalopods from Tuva have not yet been studied in detail and are known only as the list in Balashov (1962). As many as ten species have been mentioned from the Ashgillian, eleven species from the Llandoveryan. As there is not any cephalopod diversity decrease after the Ashgillian mass extinction event, the picture is similar to that known in the Siberian and Tian Shan. Thirteen species are known from the Wenlockian and six to seven species from the Ludlowian. Orthoceroids predominate in every age; euryisphonate actinoceroids are represented by the same species as in the Siberian and Mongolian assemblages.

### Conclusions

Each of the regions considered can be separated as independent biochoria of higher rank both by the taxonomic structure of communities and by the specific diversity dynamics during the Silurian.

In the tropical climatic realm (fig. 6) diversity in the Ordovician, the Llandoveryan cephalopod diversity was not lower than the Ashgillian. In the temperate and proposed polar zones Llandoveryan diversity was essentially lower than in the Late Ordovician. That means the extinction event at the Ordovician/Silurian boundary was more intensive in cold-water environments than in the tropical regions. In the Ordovician cephalopod communities were more diverse in temperate than in tropical environments. The rich and diverse communities in the Llandoveryan tropical realm (Siberian Basin) were derived from these temperate Ordovician (Baltic-like) cephalopod assemblages.

The intra-Silurian biotic event established for conodonts and graptolites was not reflected in the Silurian history of cephalopods.

The evolutionary trend towards the increase in orthoceroid diversity is observed clearly in the taxonomic structure of cephalopod communities of all the regions, and it is the global trend in cephalopod history.

### References

- Balashov, Z. G. 1962, *Ordovician Nautiloidea of the Siberian Platform*, Leningrad University Publishing House, Leningrad, 206 pp. (in Russian).
- Barskov, I. S. 1972, *Late Ordovician and Silurian Cephalopods from Kazakhstan and Central Asia*, Nauka Publishing House, Moscow, 212 pp. (in Russian).
- Barskov, I. S., Bogoslovskaya, M. F., Zhuravleva, F. A., Kisselev, G. N., Kuzina, L. F., Leonova, T. B., Shimansky, V. N. & Yatskov, S. V. 1994, 'The main morphologic event in the history of development of cephalopods in the Paleozoic', *Stratigraphy and Geological Correlation*, vol. 2 no. 1, pp. 55–61 (in Russian).
- Bogolepova, O. K. 1989, *Silurian nautiloids from the Siberian platform and their stratigraphic significance*. Candidat dissertation. Novosibirsk, 16 pp. (in Russian).
- Boucot, A. 1975, *Evolution and Extinction Rate Control*, Elsevier, Amsterdam, 300 pp.
- Kisselev, G. N. 1982, *Silurian and Lower Devonian Cephalopod Molluscs from North of the Urals*, Leningrad University Publishing House, Leningrad, 144 pp. (in Russian).
- Kisselev, G. N. 1989a, 'Silurian cephalopods of the Baltic region', *Vestnik of Leningrad University*, ser. 7 no. 1, pp. 63–66. (in Russian).
- Kisselev, G. N. 1989b, 'Cephalopod molluscs at the Silurian-Devonian boundary', *Vestnik of Leningrad University*, Ser. 7 no. 3, pp. 85–89 (in Russian).
- Kisselev, G. N. 1990, 'Classic Cephalopoda', in *Atlas of Upper Ordovician and Silurian Molluscs from the North-Western Part of the East-European Platform*, ed. G. N. Kisselev, Leningrad University Publishing House, Leningrad, pp. 33–65 (in Russian).
- Kisselev, G. N. 1992, 'Some aspects of development of cephalopods in the Silurian', *Vestnik of Leningrad University*, ser. 7 no. 3, pp. 75–83 (in Russian).
- Kisselev, G. N. 1993a, 'Silurian non-ammonoid cephalopods from Southern Tian Shan', *Vestnik of Leningrad University*, ser. 7 no. 1, pp. 21–27 (in Russian).
- Kisselev, G. N. 1993b, 'Late Silurian and Early Devonian non-ammonoid cephalopods of the western part of Southern Tian Shan', *Vestnik of Leningrad University*, ser. 7 no. 2, pp. 22–28 (in Russian).
- Kisselev, G. N., Vladimirovskaya, E. V. & Krivobrodova, A. N. 1993, 'New data on Upper Ordovician and Silurian cephalopod molluscs from Tuva', *Vestnik of Leningrad University*, ser. 7 no. 3, pp. 9–17 (in Russian).
- Miagkova, E. I. 1967, *Silurian Nautiloidea of the Siberian Platform*, Nauka Publishing House, Moscow, 56 pp.

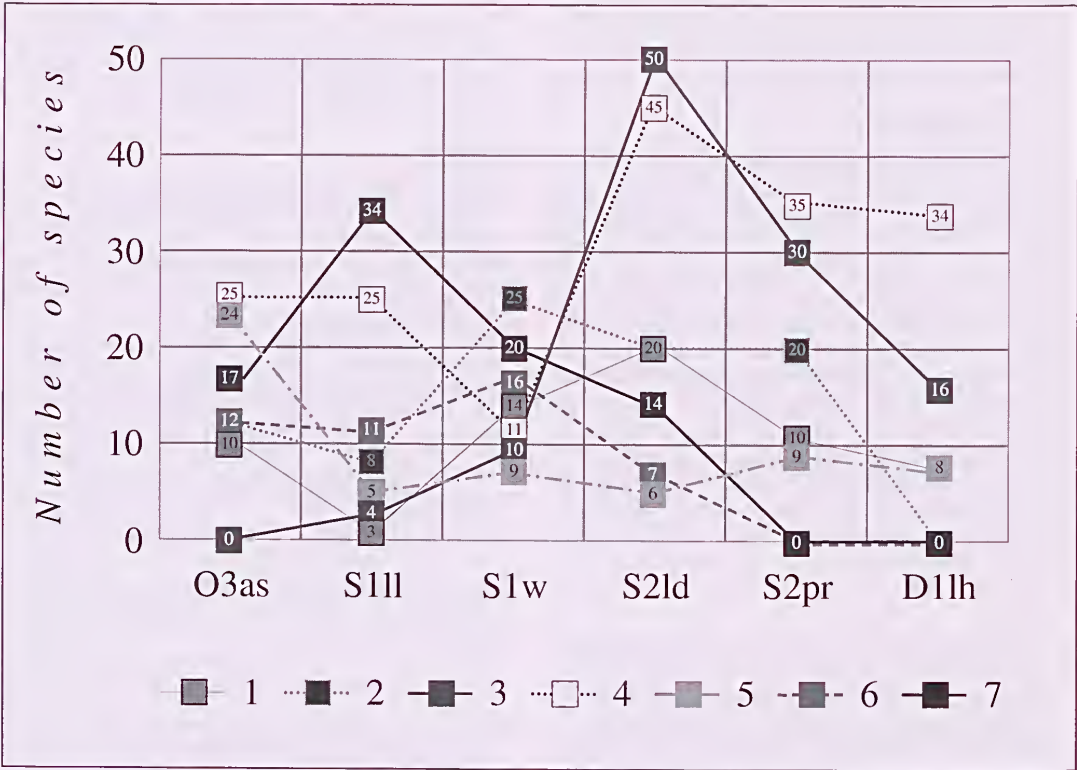
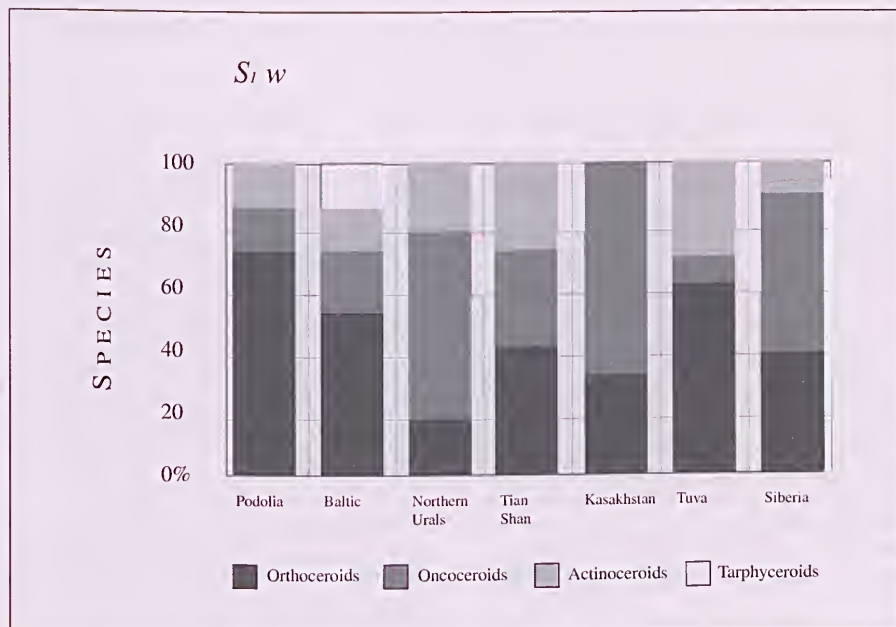


Figure 1 Changes of the specific diversity in the Silurian in different regions. Explanations in the text.



Figure 2 Taxonomic structure of the cephalopod communities in different regions in the Llandoverian. Explanations in the text.

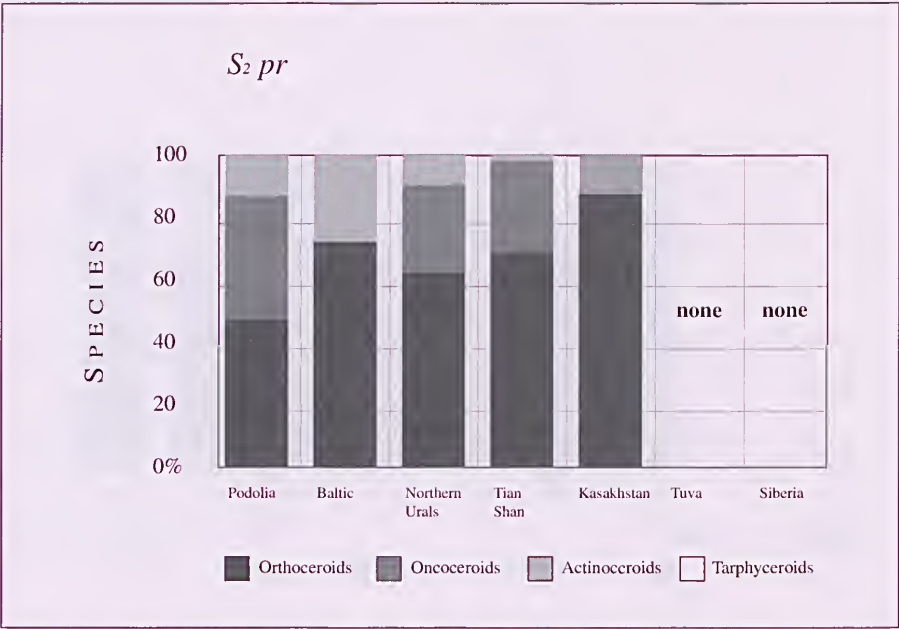




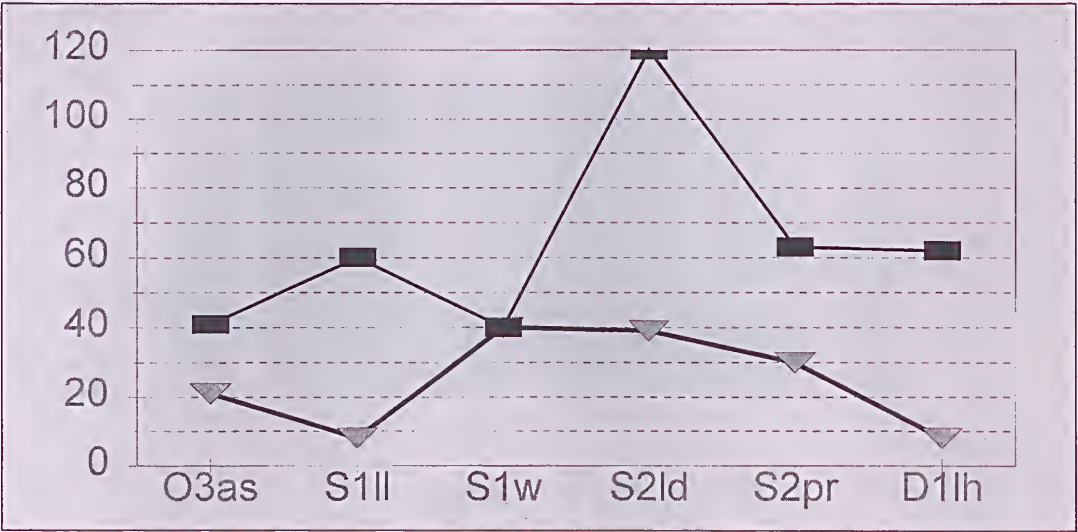
**Figure 3** Taxonomic structure of the cephalopod communities in different regions in the Wenlockian. Explanations in the text.



**Figure 4** Taxonomic structure of the cephalopod communities in different regions in the Ludlowian. Explanations in the text.



**Figure 5** Taxonomic structure of the cephalopod communities in different regions in the Pridolian. Explanations in the text.



**Figure 6** Comparison of the cephalopod diversity dynamics in the Silurian in relatively cold-water environments. Explanations in the text.

### 1.3 Brachiopod and Bryozoan Diversity During the Late Devonian Frasnian-Famennian Extinction Event

G. A. Afanasjeva, I. P. Morozova and V. N. Beznosov

The mechanisms which control both extinctions and adaptive radiations are not yet satisfactorily understood (Boucot 1990). In connection with this, it seems to us, the comparative analysis of biological changes in animals undergoing a crisis situation is of some interest.

The Late Devonian Frasnian-Famennian extinction was of a selective character. A different degree of extinction affected different marine organisms. Brachiopods and bryozoans had very different degrees of losses: brachiopods suffered most from the crisis, bryozoans, the least.

For brachiopods this extinction was one of the greatest in their history compared with that of the Late Permian. Extinction affected all taxonomic levels, including orders. The main mass of genera that appeared in the Silurian

became extinct in the Devonian. In 118 genera existing in the Frasnian, 83 perished at the end of this time (fig. 1). Two large orders, Pentamerida and Atrypida, which dominated articulate brachiopods beginning from the Ordovician, almost became extinct.

As to bryozoans during the Frasnian-Famennian event, there were no significant changes in their taxonomic composition (fig. 2). The number of those that first appeared and those that became extinct were comparable to those of other Devonian times. Changes in the taxonomic composition in Bryozoa took place mainly at the generic level. All Frasnian bryozoan orders survived into the Famennian. The total number of bryozoan genera was the same in the Frasnian and in the Famennian. In the Frasnian of the genera 105, only 14 became extinct at the end of this time.

**Figure 1** Dynamics of generic numbers of Devonian articulate brachiopods

	Lochk.	Pragnian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Orders							
Tubuliporida	6 - 0 - 0	6 - 0 - 0	7 - 1 - 0	8 - 1 - 1	10 - 3 - 2	8 - 0 - 0	8 - 0 - 0
Cystoporida	2 - 2 - 0	9 - 7 - 0	14 - 5 - 5	14 - 5 - 3	23 - 12 - 13	17 - 7 - 7	10 - 0 - 0
Trepstomida	19 - 12 - 0	23 - 4 - 0	26 - 3 - 3	34 - 11 - 7	36 - 9 - 7	31 - 2 - 5	35 - 9 - 12
Rhabdomesida	3 - 1 - 0	3 - 0 - 0	4 - 1 - 0	5 - 1 - 0	8 - 3 - 1	9 - 2 - 1	11 - 3 - 1
Fenestria	14 - 10 - 0	37 - 23 - 10	30 - 3 - 2	41 - 13 - 7	37 - 3 - 10	28 - 1 - 1	29 - 2 - 0
Cryptostomida	1 - 0 - 0	2 - 1 - 1	4 - 2 - 1	5 - 2 - 0	6 - 1 - 1	5 - 0 - 0	5 - 0 - 0
Phylloporinida	?	?	?	?	1 - 1 - 0	?	?
Ctenostomida	6 - 0 - 0	6 - 0 - 0	6 - 0 - 0	7 - 1 - 0	7 - 0 - 0	7 - 0 - 0	7 - 0 - 1
Total	57 - 25 - 0	86 - 35 - 11	91 - 15 - 11	114 - 34 - 18	128 - 32 - 34	105 - 12 - 14	105 - 14 - 14

In every column first cipher means total number of genera, second number of first appeared genera, third number of extinct genera.

**Figure 2** Dynamics of genera of Devonian bryozoans

Age	Lochk.	Early Pragnian	Emsian	Middle Eifelian	Givetian	Late Frasnian	Famennian
Orders							
Orthida	23 - 6 - 9	17 - 3 - 3	16 - 2 - 7	16 - 7 - 9	8 - 1 - 0	10 - 2 - 7	3 - 0 - 0
Strophomenida	37 - 16 - 11	36 - 10 - 8	39 - 11 - 16	36 - 13 - 9	27 - 10 - 9	17 - 9 - 14	23 - 20 - 21
Chonetida	8 - 5 - 2	22 - 16 - 9	33 - 14 - 22	16 - 5 - 9	8 - 1 - 5	6 - 3 - 3	4 - 1 - 2
Productida	-	1 - 1 - 0	3 - 2 - 2	7 - 6 - 3	7 - 3 - 3	5 - 1 - 3	23 - 21 - 18
Pentamerida	8 - 4 - 4	8 - 4 - 2	16 - 10 - 1	16 - 1 - 8	10 - 2 - 6	7 - 3 - 7	-
Rynchonellida	27 - 17 - 6	35 - 14 - 13	37 - 15 - 14	33 - 20 - 20	28 - 15 - 19	22 - 13 - 18	27 - 23 - 24
Atrypida	18 - 5 - 6	18 - 6 - 2	21 - 5 - 6	25 - 10 - 17	8 - 0 - 4	4 - 0 - 4	-
Spiriferida	30 - 12 - 7	38 - 15 - 9	59 - 30 - 26	48 - 15 - 26	33 - 11 - 11	32 - 10 - 23	23 - 14 - 17
Athyrida	21 - 13 - 8	21 - 8 - 9	25 - 13 - 11	23 - 9 - 8	18 - 3 - 10	12 - 4 - 7	11 - 6 - 3
Terebratulida	-	1 - 1 - 0	8 - 7 - 6	6 - 4 - 1	14 - 9 - 12	3 - 1 - 1	2 - 0 - 1
Total	172 - 78 - 53	197 - 78 - 55	257 - 109 - 111	226 - 90 - 120	161 - 55 - 89	118 - 46 - 87	116 - 85 - 86

In every column first cipher means total number of genera, second number of first appeared genera, third number of extinct genera.



Brachiopoda and Bryozoa are united by many common characters of their biological organization and even are referred by many biologists to a single group — Tentaculata or Lophophora. They are both fixed filter feeders and belong to the same trophic (sestonophages) and etological (epibionts) types. In the Late Devonian both brachiopods and bryozoans populated diverse shallow-water environments. However, as we can see, even though these two invertebrate groups are so similar, they reacted differently to the Frasnian–Famennian crisis.

Frasnian–Famennian extinctions took place against a background of large-scale marine regressions. The rate of the sea level fall at the end of Frasnian was the greatest in the Phanerozoic (Hallam 1984; McGhee 1990, 1992). One of the explanations for this event is connected with a large meteorite impact of the Earth, which caused a giant tidal wave globally and a subsequent period of turbid water. Many benthic filtrators living on mud and sandy bottoms suffered (McLaren 1982 et al.). We think that the situation after impact could have been much more complicated. It is obvious that besides raising the level of turbidity, the collision, first of all, was accompanied by strong disturbance of the vertical structure of the ocean, which had, as consequences, forcing deep water to the surface, a dramatic lowering of the temperature of the surface waters and dramatic changes of ocean chemistry, such as salinity and the oxygen regime. It also raised from near bottom layers of detrital masses and because of this possibly toxified the surface waters.

The reasons for a high level of survival of bryozoans in comparison to brachiopods in these conditions may relate to the greater tolerance of bryozoans, which are rather tolerant of the lowering of temperature and salinity and to changes of oxygen regime of water and also in adaptive advantages, which bryozoans obtained with colonial organization.

Every colony of Bryozoa, both living and fossil, represents a qualitative system distinguished from other colonial groups by a peculiar display of its integrity. It is typical for bryozoans to have joint metabolism within a colony and wide communication of coeloms of all zooids by means of different types of connecting pores. Zooids compounded in a colony are different in their structure and physiology and each of them fulfills a strictly definite function, such as nutrition, reproduction, protection, etc. Thus, the functioning of every individual in the colony is directed to be of benefit to the whole colony. Microscopic size of zooids and a short life cycle in comparison with that of the colony and also the ability for regular degeneration and regeneration of polypids are important distinguishing characters of the bryozoan colony. At the place of an atrophied polypid a new polypid is formed, often for another functional purpose, which is more appropriate to necessities of the whole colony. Bryozoans also differ from other colonial groups in the relative small size of their colonies, which permits them, using minimal food resources, to occupy diverse niches in complicated

marine biotopes. Many fenestellids, which flourished at the Late Devonian, were supplied with special tubercles situated in the peristome of the aperture of zoocidium and this had the function of strengthening and supporting a lophophore (Snyder 1991). Colonies of the latest Late Devonian bryozoans were raised a little above the substratum. The number of feeding polypids could change in connection with changes of conditions. It is possible that the number and size of the tentacles of the lophophore were also variable, as is observed in recent bryozoans, depending on a quantity of food resources (McKinney 1990). No doubt, that high degree of colonial integrity of bryozoans and the peculiar plasticity of zooids promoted their surviving a crisis situation.

It is natural that stenobiont brachiopods suffered much more than bryozoans with changes of environmental conditions. All living articulate brachiopods are confined to water of open marine salinity, and they are not tolerant to changes of temperature and oxygen regime or of quality and quantity of food (Rudwick 1970). Among brachiopods, forms with a poorly protected internal shell cavity of harmful particles, perished first of all. This can explain the disappearance of atrypids at the end of the Frasnian. Atrypids were especially widespread in the varied shallow-water and off-shore marine zones before the crisis (Copper 1966, 1977). At the end of the Frasnian, they all perished, and their niches were occupied by the rhynchonellids. The reason for this could be connected with a character of specialization of the filter feeding system in brachiopods of these two orders.

In atrypids the filter feeding system was complex and the lophophore enlarged. The origin of calcareous spiral brachidium in brachiopods, which strengthened the lophophore, was connected with the appearance of atrypids at the Middle Ordovician. Further evolution of all atrypids went in the direction of enlargement and complication of spiral brachidium. However, possessing a powerful filter feeding system, these brachiopods did not have an effective protection of the internal cavity of the shell against harmful particles. Rhynchonellids had a weaker lophophore. The spiroloph of rhynchonellids was smaller in size and in the number of volutions than that of atrypids and was supported mainly by hydrostatic pressure. However, the protection of the internal shell cavity against ingress of harmful particles, 'littering' of the lophophore, in these brachiopods was minimized successfully by means of zigzag deflexion of anterior margins of the valves. Apparently there was increased protection of the mantle cavity and lophophore without reduction of gape space of the shell (Rudwick 1970). At the same time, the filter feeding process was improved, as zigzag deflections permitted the gape space to remain large enough without enlargement of the gape angle and allowed a more successful gathering of food. It seems that just these adaptations gave to rhynchonellids definite advantages in the turbid conditions of shallow water environments and was a reason for their crowding out of the atrypids during the Frasnian–Famennian crisis.

## References

- Boucot, A. J. 1990, *Phanerozoic extinctions: how similar are they to each other? Extinction events in earth history*, eds. E. G. Kauffman, O. H. Walliser. Lecture notes in earth sci., 30, Springer-Verlag, Berlin, pp. 5–30.
- Copper, P. 1966, 'Ecological distribution of Devonian atrypids brachiopods', *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 2 no. 3, pp. 245–266.
- Copper, P. 1977, 'Palaeolatitudes in the Devonian of Brazil and Frasnian-Famennian mass extinction', *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 21 no. 3, pp. 165–207.
- Copper, P. 1986, 'Evolution of the earliest smooth spire-bearing atrypoids', *Palaeontology*, vol. 29 no. 4, pp. 827–866.
- Hallam, A. 1984, 'Pre-Quaternary sea-level changes', *Annual Review of Earth and Planetary Sciences*, no. 12, pp. 205–243.
- McGhee, G. R. 1990, 'Mass extinction: Events. Frasnian-Famennian', in *Palaeontology: A synthesis*, ed. D. E. G. Briggs & P. R. Crowther Blackwell, Oxford, pp. 184–187.
- McGhee, G. R. 1992, 'Evolution biology of Devonian Brachiopoda of New York State: no correlation with rate of change of sea-level?', *Lethaia*, vol. 25, pp. 165–172.
- McKinney, F. K. 1990, 'Feeding and associated colonial morphology in marine bryozoans', *Critical Reviews in Aquatic Sciences*, vol. 2 iss. 2, pp. 255–280.
- McLaren, D. 1982, 'Frasnian-Famennian extinctions', *Special Paper of the Geological Society of America*, no. 190, pp. 447–484.
- Rudwick, M. J. S. 1970, *Living and fossil brachiopods*. Hutchinson, London, 199 pp.
- Snyder, E. M. 1991, 'Revised taxonomic procedures and paleoecological applications for some North American Mississippian Fenestellidae and Polyporidae (Bryozoa)', *Paleontographica Americana*, no. 57, 275 pp.





## 1.4 Diversity Dynamics in the Order Trepostomida (Bryozoa)

R. V. Gorjunova, A. V. Markov and E. B. Naimark

### Abstract

The dynamics of the quantitative parameters in the evolution of Trepostomida makes it possible to distinguish the phases of growth, acme and decline in the development of the trepostomid suborders. During the Paleozoic the percentage of euryoecic genera increased continuously due to the replacement of the genera with low level of polymorphism by the genera with well-developed polymorphism. The increase of diversity in the Famennian and Permian, as well as survival across the Permian–Triassic boundary can be explained by the higher tolerance of the trepostomids to the environmental changes compared with other groups of Paleozoic bryozoans.

### Introduction

Trepostomida is the largest order of Paleozoic bryozoans. It is comprised of more than 130 genera. The order is well defined morphologically and is characterised by well-developed polymorphism (Astrova 1978; Gorjunova 1992; Gorjunova et al. 1994). The trepostomids appeared in the Early Ordovician (Arenig) and became extinct at the end of the Triassic.

This analysis of trepostomid generic diversity dynamics has been based on the new methods of the systemic and statistical studies of the macroevolutionary process (Markov & Naimark 1994a-d, 1995).

### Material and Methods

We have used data on taxonomy, geographical and stratigraphic distribution of all the genera of the trepostomids. Computer software was used to make the calculations. The basic theoretical model of the taxonomic evolution applied here is described in the paper by Markov and Solovjev (this volume). The main quantitative parameters used — the geographical distribution index of genera (GDI) and generic longevity (L) are explained there also. The average generic GDI and L show the average level of tolerance, or 'euryoky' of genera. The integral GDI and L can be used as the estimations of the total volume of the resource space

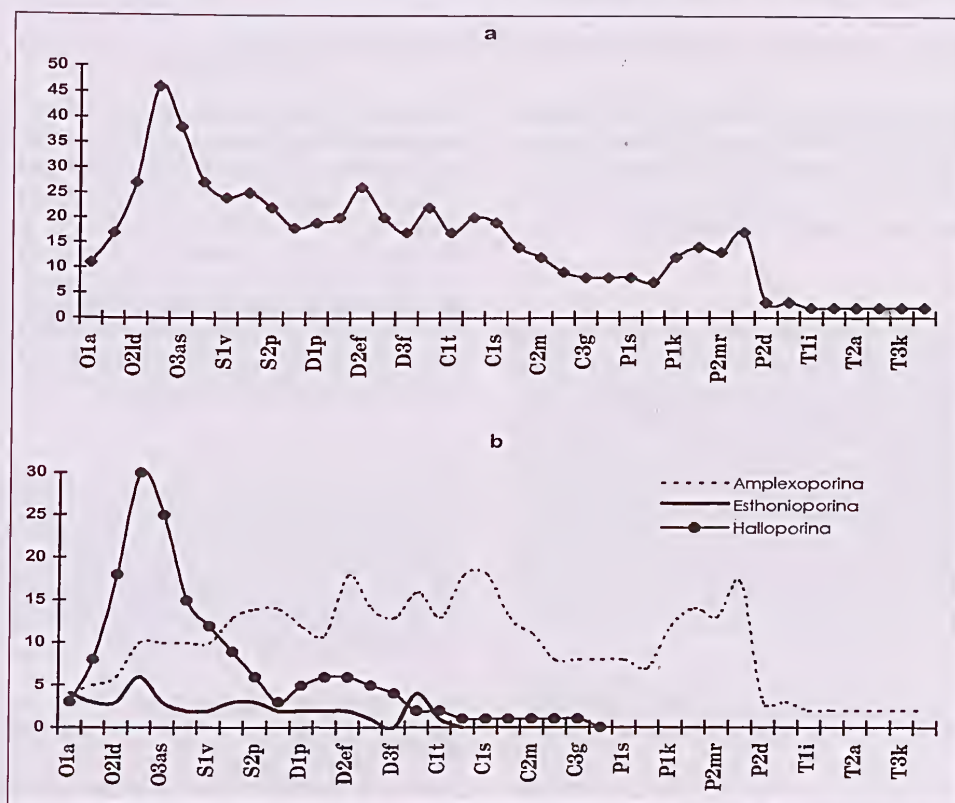


Figure 1 The generic diversity in the Trepostomida. (a) all the order; (b) three suborders.

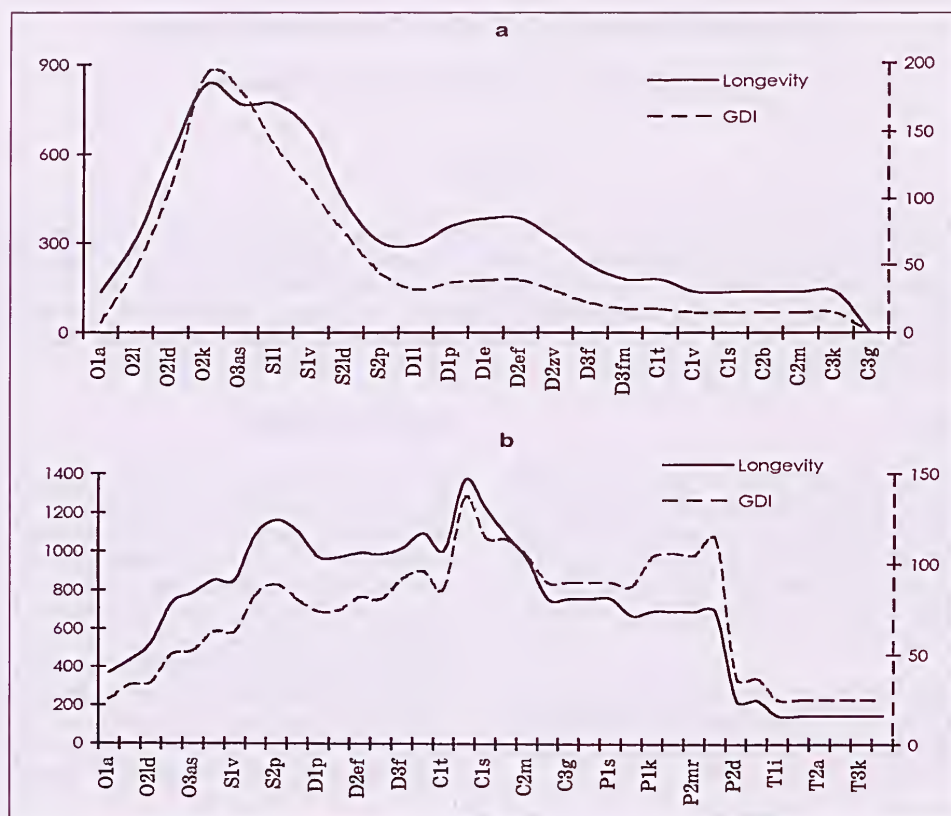


Figure 2 Integral Geographical Distribution Index and Longevity in the *Halloporina* (a) and *Amplexoporina* (b).

occupied by the group (integral niche size). We also used the point of 50% extinction of genera (p): this parameter is similar to L, but sometimes it is more precise.

### The main stages of trepostomid evolution

#### Ordovician

The oldest trepostomid genus is *Esthoniopora* from the Early Arenig. Generic abundance of this group increased rapidly during the Early Ordovician (there were 10 genera by the end of the epoch) (fig. 1a). By this time all the three suborders (*Esthoniopora*, *Halloporina*, *Amplexoporina*) already existed (fig. 1b). The increase of the integral GDI and L demonstrates the wide expansion of the group (fig. 2). There was no extinction at the generic level during the Early Ordovician. Divergence of genera was mostly of extensive type (new genera occupied new niches). Most of the new genera were broadly tolerant (euryoecic).

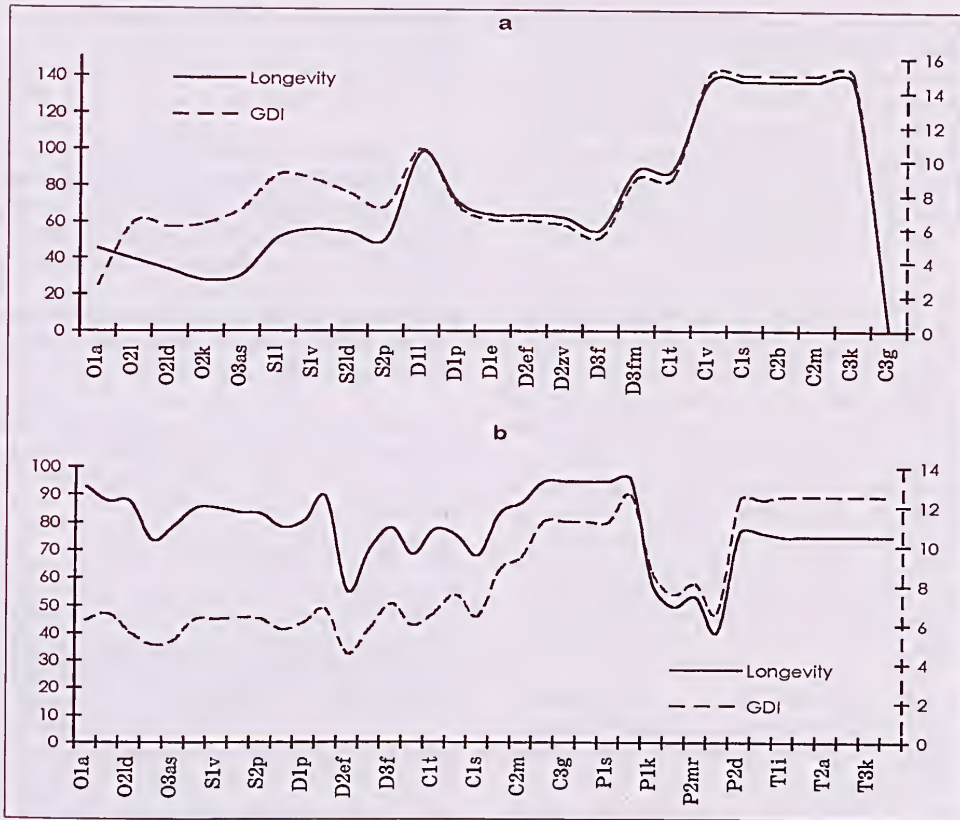
In the Middle Ordovician, 30 more genera appeared (19 of them in the Caradoc). During the Ashgillian, the rate of origination of genera suddenly decreased (only three new genera appeared). The average GDI and L decreased (fig. 3). The integral GDI and L reached their maximum in the Caradoc (fig. 2). The genera with first occurrences in the

Caradoc were rather short-lived ( $p=16.7$  mln.y). All these show that the phase of extensive divergence had finished, and the period of intensive divergence had begun. Competition between the genera increased, and it stimulated the specialisation and splitting of the niches (Schmalgause 1939). Comparison of generic longevity in genera with different types of polymorphism has shown that the development of the tetramorphic colonies was the most advantageous (genera became more tolerant), while the transfer from dimorphic colonies to trimorphic had a much smaller effect.

During the Middle and Late Ordovician the suborder *Halloporina* was at its acme (climax); the most primitive and specialised suborder *Esthoniopora* was already in the phase of decline, while the most progressive suborder *Amplexoporina* was still in the phase of extensive divergence. By the end of the Ordovician the independent development of the two main suborders (*Halloporina* and *Amplexoporina*) had become obvious.

The extinction rate increased greatly during the last two ages of the Ordovician (11–13 extinct genera per age). There was also a selective extinction of specialised forms (Markov & Naimark 1994d). The extinction rate was much greater in the *Halloporina* than in the *Amplexoporina*. This extinction does not necessarily





**Figure 3** Average Geographical Distribution Index and Longevity in the suborders of the trepostomids. (a) *Halloporina*; (b) *Amplexoporina*.

suggest some great environmental change at the end of the Ordovician, because even some minor changes may have been enough to provoke the extinction of specialised taxa.

### Silurian

During the Silurian nine new genera appeared; their average GDI and L were the highest; ( $p=39.3 \text{ mln.y}$ ). This is a typical character of the phase of extensive divergence. Yet the total number of genera decreased, as well as the integral GDI and L (this is typical during the phase of decline).

The generic diversity of the Esthonioporina decreased during the Silurian up to 1–2 co-existing genera. This suborder had become a relict group. The generic abundance of the Halloporina decreased by 75%. Almost all the new genera were amplexoporins. In this suborder the integral GDI and L were increasing and the average GDI and L did not decrease.

It is difficult to evaluate the influence of the environmental factors on the trepostomid evolution during the Silurian. The environmental conditions were the same (presumably good) for all bryozoans, yet the esthonioporins became a relict group, halloporins were in

the phase of decline, while the amplexoporins were in the phase of extensive divergence. These facts are more easily explained by the evolutionary correlation at the taxonomic level, provided the taxa are regarded as integral self-organising systems.

### Devonian

The total generic abundance increased during the Devonian. The rate of generic differentiation was several times lower in the Early Devonian, Zivetian and Frasnian (2 genera per stage/age on average) than in the Eifelian (7 genera) and the Famennian (10 genera). The genera with first occurrences in the Devonian were on average short-lived ( $p=19.6 \text{ my}$ ) and inhabited small areas (they were mostly endemic). Correspondingly, there are distinct minimums on the curves of the average generic GDI and L in the Eifelian and the Famennian. The outbursts of generic differentiation were accompanied by the decrease of the average level of generic tolerance (increase of specialisation). The contract between the distinct peaks on the curve of generic abundance in the Eifelian and the Famennian and the almost total lack of any increase on the curves of the integral GDI and L shows that the divergence of the trepostomid genera was mostly of intensive type (there was no expansion and no occupation of the vacant niches). The extinction and

origination rates changed synchronously. All this gives a typical picture of the fluctuations of diversity around a stable average level, which is characteristic of the taxa in the phase of acme (climax). The transfer of the Amplexoporina from the phase of extensive divergence into the phase of acme was not accompanied by tachytely (as in the Halloporina during the Ordovician). It was occurring according to the principle of bradytely (gradual increase of diversity without excessive specialisation).

What were the reasons for the outburst of the intensive divergence in trepostomids in the Eifelian and the Famennian? During the Eifelian the diversity increased almost in all the large taxa of marine invertebrates. This strongly suggests some common (external) reasons for these events (for instance, the expansion of the warm shallow-water seas). Probably during the Eifelian the competition between the trepostomids and other bryozoan orders decreased. This could have stimulated the intrageneric competition within some groups of the Trepostomida. Actually the intensive divergence in the Eifelian took place only in the subfamily Eridotrypelinac (Amplexoporina); all the other groups were not involved in the process.

There was quite a different situation in the Famennian, when the generic abundance became distinctly lower in many groups of invertebrates (Rugosa, Brachiopoda; several bryozoan orders). Yet some other groups demonstrated a rapid increase of diversity; among them are the ammonites and the bryozoan orders Trepostomida and Rhabdomesida. The environmental changes at the end of the Devonian (the decrease of shelf and littoral areas) contributed to the demise of the trepostomid's competitors (fenestellids and cystoporids). It stimulated the mass origination of specialised, vulnerable and short-lived genera. The trepostomids appeared to be more tolerant of the environmental changes at the end of the Devonian, presumably because they were more eurybathic than the other Bryozoans.

### Carboniferous

The origination of genera in the Early Carboniferous was of quite another type than that in the Eifelian and the Famennian. During the Tournaisian and the Visean the extensive divergence resumed in the Amplexoporina; some innovation can be detected also in the relict groups (Halloporina, Esthonioporina). The genera with first occurrences in the Tournaisian and the Visean were long-lived and inhabited large areas ( $p=40.5$  mln. y.;  $GDI=6$ ). Average and integral  $GDI$  and  $L$  increased, which means the expansion of the order and the occupation of the new niche was occurring. This expansion could have been stimulated by a marine transgression. The generic diversity during the Early Carboniferous was increasing in all large bryozoan orders, and also in corals, brachiopods, cephalopods, etc.

In the Middle and Late Carboniferous the rate of generic

origination decreased greatly. The trepostomids were now in decline.

### Permian

At the beginning of the Permian the generic abundance of the Trepostomida continued to decrease. The extinction was selective: specialised genera became extinct, while the tolerant ones survived. Probably the decline of the trepostomids in the Late Carboniferous and Early Permian was stimulated by the pressure of the competitors (the cystopodid family Cystodictyonidae with bifoliate colonies and the fenestellids with bilateral colonies and ovicells).

In the Kungurian the rate of generic origination abruptly increased. By the end of the Midian 13 new genera appeared. Then the generic origination stopped completely.

The generic divergence in the Middle Permian was distinctly intensive. The new genera were very short-lived; their areas were small; the increase of the generic diversity was accompanied by the synchronous decrease of the average  $GDI$  and  $L$ . The new genera appeared through specialisation and splitting of the niches.

Probably the reasons for the successful competition of the trepostomids with other bryozoans in the middle of the Permian can be found in the specific features of their phylogeny at this time. The trepostomids had simple colonies and no brood chambers, yet they could have taken some advantage from their polymorphism (akanthozooecia and exilazooecia). In the middle of the Permian the number of akanthozooecia and exilazooecia in the trepostomid colonies increased greatly; and these structures themselves became larger and more differentiated. Typical examples are *Dyscritella*, *Dyscritellina* and *Araxopora*. Therefore, the trepostomid evolution tended to intensify the function of the structures already obtained. Probably the well developed polymorphism and the ability to live at various depths aided their survival at the Permian-Triassic boundary (as most bryozoans and many other invertebrates did).

### Triassic

During this final stage of their evolution the trepostomids were a relict group. The last trepostomids died out at the end of the Triassic.

### Conclusion

The diversity dynamics curve of the trepostomids (fig. 1a) is not a regular domed curve, which is typical for the development of integral taxonomic systems. Yet it can be divided into two rather regular domed curves of the two main suborders (*Halloporina* and *Amplexoporina*), each of the two forming an integral system of its own (fig. 1b).



The intensive divergence in the Trepotomida during the Famennian and Permian, when the diversity of the fenestellids and cystoporids was decreasing, shows that the evolution of different bryozoan orders in the Paleozoic could have been interdependent.

During the Paleozoic the percentage of euryoecic genera increased continuously due to the replacement of the genera with a low level of polymorphism by the genera with well-developed polymorphism.

The increase of diversity in the Famennian and Permian, as well as survival across the Permian–Triassic boundary can be explained by the broader tolerance of the trepotomids of the environmental change.

## References

- Astrova, G. G. 1978, 'The history, taxonomy and phylogeny of the bryozoans. Order Trepotomida', *Science*, 240 pp. (in Russian).
- Gorjunova, R. V. 1992, 'The system of the Paleozoic bryozoans', *Science*, 168 pp.
- Gorjunova, R. V., Markov, A. V. & Naimark, E. B. 1994, 'The stages of evolutionary development of the trepotomid Bryozoans', *Jour. General Biology*, vol. 4–5, pp. 489–508 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994a, 'The survivorship curves as a proof of the reality of high taxa', *Paleontol. J.*, vol. 2, pp. 3–11.
- Markov, A. V. & Naimark, E. B. 1994b, 'The dynamics of the phylogenetic processes in supraspecific biosystems', *Paleontol. J.*, vol. 3, pp. 3–12 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994c, 'The study of the diversity dynamics of the high taxa by means of mathematic modelling', *Jour. General Biology*, vol. 3, pp. 303–317 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994d, 'The selective extinction of specialised taxa and its role in the evolution of biota', *Jour. General Biology*, vol. 6, pp. 673–683 (in Russian).
- Markov, A. V. & Naimark, E. B. 1995, 'The relation between the level of diversity of high taxa and the degree of specialisation of genera and species (illustrated by some groups of Paleozoic invertebrates)', *Jour. General Biology*, vol. 1, pp. 97–107 (in Russian).
- Schmalgausen, I. I. 1939, 'The patterns and the regularities of the evolutionary process', *USSR Acad. Sci. Publ.*, 231 pp. (in Russian).



# 1.5 Changes of the Generic Diversity of Marine Bryozoans (Triassic – Recent)

L. A. Viskova

This paper traces the changes of the generic diversity historical development of marine bryozoans: Stenolaemata from Triassic to Recent interval and the calcareous Eurystomata (Cheilostomata) from the Late Jurassic–Recent.

All data (some not yet published) on genera of numerous bryozoan collections from the Jurassic–Neogene of different regions of the former USSR and some other countries which are housed at the Palaeontological Institute in Moscow are dealt with in this paper. Corrections to information included in *Treatise on Invertebrate Paleontology on Bryozoa* (Bassler 1953) are included in this paper. For example, changes were introduced for higher taxa to the ordinal level (Viskova 1992), and more precise information was obtained on geological distribution of the majority of genera. The number of genera, both fossil and recent, has been noticeably increased, and some genera, which previously had been considered as synonyms have been split (Berthelsen 1962; Brood 1972; Buge 1957; David, Mongereau, Pouyet 1972; Keij 1972; Taylor 1986, 1994; Viskova 1972; Voigt 1967; 1987; 1989; Voigt, Hillmer 1983 et al.) since the *Treatise* volume was published.

Although the total number of genera may be overstated, it does not negate their general tendency to diversification in geological time. On the whole, the present state of the study of the Mesozoic–Cenozoic skeletal bryozoans allows the following conclusions.

Bryozoans in the class Stenolaemata, represented after the Permian–Triassic crisis only by a few Paleozoic genera (Schaefer & Foisc 1987; Taylor & Michalik 1991; Viskova & Morozova 1993) underwent their first noticeable radiation in the Middle Jurassic, when stable conditions of life in the marine basins had been established. At that time the new order Melicerititida arose, new genera were added to both the order Tubuliporida, that survived the Permian–Triassic boundary, and the order Cerioporida, which evidently arose in the Middle Triassic (Viskova 1980, 1992; Viskova & Morozova 1993; Walter 1969). Until near the end of the Middle Jurassic all of these Stenolaemata were the only bryozoans with calcareous skeletons.

Mesozoic–Cenozoic skeletal bryozoans of the class Eurystomata appeared at the beginning of the Late Jurassic (Taylor 1994a) with the first genus being

Figure 1 Stenolaematans in the Triassic – Recent interval

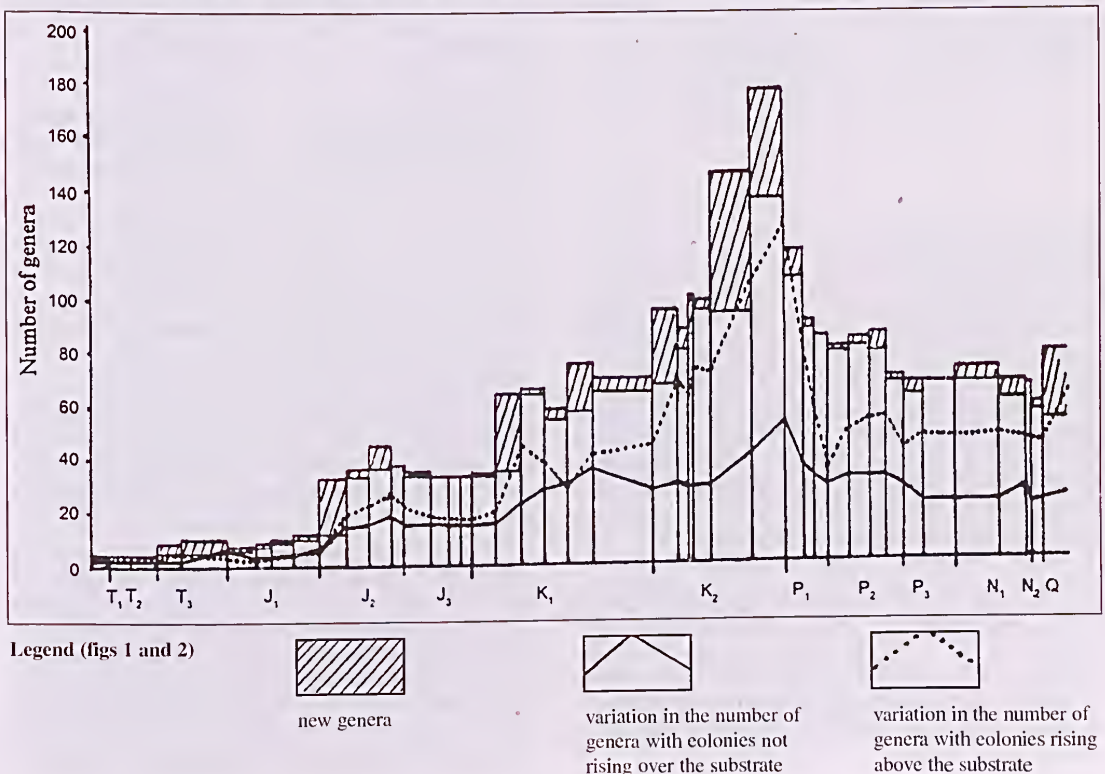
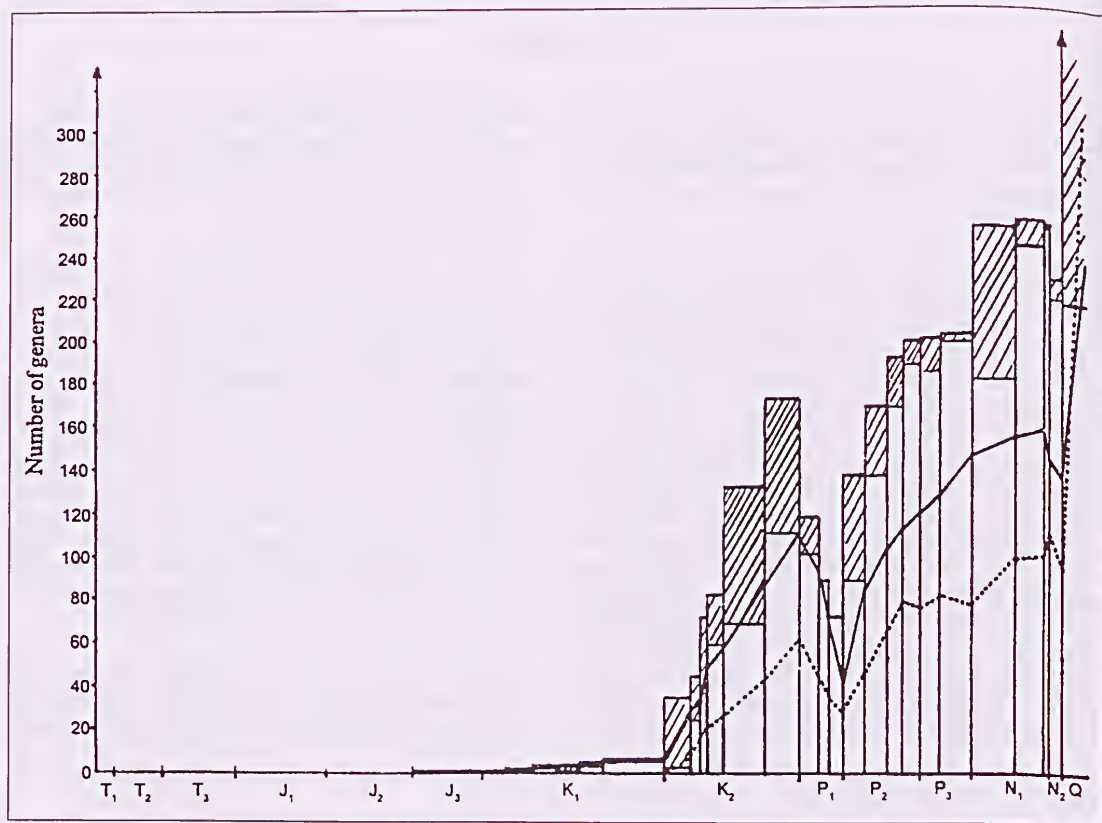


Figure 2 Calcareous eurytomatans in the Late Jurassic — Recent interval



Legend (figs 1 and 2)



new genera

variation in the number of  
genera with colonies not  
rising over the substratevariation in the number of  
genera with colonies rising  
above the substrate

*Pyriporopsis* Pohowsky, 1973 of the order Membraniporida. It should be noted that in the evolution of the Eurytomata the ability to produce a calcareous skeleton developed twice (first with the Paleozoic fenestellids). With the exception of the order Flustrida, which arose in the Early Cretaceous (Lidgard, McKinney & Taylor 1993; Taylor 1986), all other eurytomatous orders appeared in the Late Cretaceous: Cribrilinida, Microporida, Cellariida, Skyloniida — at the beginning of this time, and Scrupariida, Bugulida (suborder Scrupocellariina), Catenicellida — at the end of it (Viskova 1992; Viskova & Morozova 1993).

On the whole, the Late Cretaceous was characterised by further development of stenolaematous and eurytomatous bryozoans. Nearly all of the above-mentioned orders, with the exception of the Melicerititida and Skyloniida, which became extinct respectively in the Paleogene and in the Pliocene, are still flourishing in present marine basins.

Comparisons of a number of genera in both classes of bryozoans in every subdivision of the Late Jurassic–Late Cretaceous interval show the consecutive increase in their diversity until the end of the Cretaceous (figs 1, 2). It is noticeable that the number of genera in the Stenolaemata was somewhat reduced during some time intervals (fig. 1). Evidently such diversity decrease was connected to unfavourable environmental conditions, but the eurytomatous bryozoans seem to be unaffected. Their diversity increased incessantly without interruption (fig. 2).

Nevertheless, in the Maastrichtian the Stenolaemata reached the peak of their generic diversity — 176 genera (fig. 1). It was the greatest diversity in their entire history from the beginning of the Mesozoic to the Present. The generic diversity of the skeletal eurytomatans in the Maastrichtian was nearly as great — 173 genera (fig. 2). Such quantitative data of generic diversity for bryozoans in both classes challenges the idea that up to the end of the



Late Cretaceous the skeletal Eurystomata (=Cheilostomata) with their rapid diversification predominated over the Stenolaemata and began to supplant them in the Campanian and Maastrichtian (Lidgard, McKinney & Taylor 1993; Viskova 1980, 1992; Viskova & Morozova 1993; Voigt 1981, 1985).

The response of stenolaematous and eurystomatous bryozoans to the Cretaceous–Paleogene crisis was evidently dramatic but not catastrophic. As shown above, both groups arrived at the Cretaceous–Paleogene boundary with about an equal generic diversity. There were many genera among them distinguished by their narrow morphological specialisations, apparently connected with the very specific ecological adaptation. Environmental conditions changed dramatically at the end of the Maastrichtian nearly everywhere because of global cooling which caused fluctuations of the sea level. Extinction of specialised bryozoans, which were very sensitive to environmental change was inevitable.

It is interesting to notice that in both classes a number of genera became extinct in the Maastrichtian and of those that survived into the Danian, the number of genera evolving and dying out during the Paleocene was roughly the same. On the whole by the end of the Thanetian, the number of genera in those classes was reduced more than double compared with the situation in the Maastrichtian (figs 1, 2).

Generic diversity of the Stenolaemata (Bassler 1953; Bock 1993, Brood 1972; Buge 1957; D'Hondt 1982; Kluge 1962; Pitt & Taylor 1990; Ponomareva 1987; Taylor 1994b; Vavra 1977; Viskova 1972, 1980; Voigt 1967, 1981, 1985, 1987; Weiss 1988 et al), with some fluctuations, remained similar to that at the end of the Paleocene and during their continued evolution up to Present. In the Recent marine basins of the 77 genera known, 51 of them are relicts of the Mesozoic–Cenozoic seas and 26 genera appeared only recently, in the present in the Holocene (fig. 1).

The generic diversity of eurystomatous bryozoans (Bassler 1953; Berthelsen 1962; Bock 1993; Buge 1957; Cook & Chimonides 1986; D'Hondt 1981; Favorskaya 1988, 1992; Gordon 1989; Hayward & Ryland 1979; Larwood 1962; Pouyet 1965; Ryland & Hayward 1977; Vavra 1977; Voigt 1967, 1987, 1989; Voigt & Hillmer 1983; Weiss 1988 et al), after noticeable reduction of it in the Paleocene, increased rapidly during the Eocene–Present epochs. The Eurystomata became predominant over the Stenolaemata in Cenozoic seas, from Eocene times onward (fig. 2). In recent marine basins they continue to undergo divergence and adaptive radiation: there are now over 500 genera of skeletal eurystomatans, more than half of them (288 genera) are known only in present seas, the remaining known as fossils from Cretaceous and Tertiary deposits.

Analysis of growth-forms of bryozoans in both classes,

reduced for the sake of simplicity, come in two main types — those that rise above the substrate and those that lie closely associated with it. Stenolaematans attached to the substrate by a small base and branching into the water began to predominate over those flat-lying forms from the Middle Jurassic up to the Present (fig. 1). On the contrary in eurystomatous colonies different types of flat-lying colonies were predominant over those forms rising above the substrate during their whole geological history (fig. 2); the branching forms dominate only in today's seas. Such correlation of life-forms of bryozoans of both classes allowed them to develop parallel and without any obvious competition.

On the whole, evolutionary success of eurystomatous bryozoans, young when compared to the more ancient stenolaematans, was connected undoubtedly with the refinement of their colonial organisation. Morphological changes that took place in colonies of stenolaematous bryozoans during their history did not alter their basic plan of tubular zooids. On the contrary, in eurystomatans noticeable morphological reorganisations affected their basic plan of zooids: clear differentiation of the walls, development of a complicated system of pore chambers and plates, changes in the structural features of the frontal walls, etc. The diversity of morphofunctional and positional polymorphism considerably distinguishes eurystomatans from stenolaematans. All of these changes and innovations increased the breath of variation of colonial organisation in eurystomatous bryozoans and added to their adaptability. As a result, they could cope better with fluctuations of the biotic and abiotic nature and thus colonized the new niches, which were inaccessible to the majority of the Stenolaemata, with their more simple stereotyped organisation, thus giving rise to their present success reflected by diversity.

## References

- Bassler, R. S. 1953. Treatise on Invertebrate Paleontology. Part G Bryozoa. Geol. Soc. Amer. and Univ. Kansas Press, Lawrence, pp. 1–253.
- Berthelsen, O. 1962. 'Cheilostome Bryozoa in the Danian deposits of East Denmark', *Danmarks Geologiske Undersøgelse*, vol. 83, pp. 1–290.
- Bock, P. 1993. Checklist for Recent Bryozoans of Australia, Melbourne, pp. 1–23.
- Brood, K. 1972. 'Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia', *Acta Univ. Stockholm. Contrib. Geol.*, vol. 26, pp. 1–464.
- Buge, E. 1957. 'Les Bryozoaires du néogène de l'Ouest de la France et leur signification stratigraphique et paléobiologique', *Mem. Mus. Nat. hist. natur.* Ser. C, vol. 6 no. 1, pp. 1–436.
- Cook, P. L. & Chimonides, P. J. 1986. 'Recent and fossil Lunulitidae (Bryozoa: Cheilostomata)' *Journ. Natural History*, vol. 20, pp. 681–705.
- David, L., Mongereau, N. & Pouyet, S. 1972. 'Bryozoaires du néogène du bassin du Rhône', *Docum. Lab. Geol. Fac. Sci. Lyon*, no. 52, pp. 1–118.
- D'Hondt, J. L. 1981. 'Bryozoaires cheilostomes bathyaux et abyssaux provenant des campagnes océanographiques américaines (1969–1972) de l' "Atlantis-2", du "Chain" et du "Knorr" (Woods Hole Oceanographic Institution), *Bull. Mus. nat. hist. natur.*, Ser. 4, vol. 3 (A) no. 1, pp. 5–71.

- D'Hondt, J. L. 1982, 'Bryozoaires cyclostomes bathyaux des campagnes oceanographiques de L "Atlantis-2", du "Chain" et du "Knorr" (1967-1972)', *Bull. Mus. nat. hist. natur.*, Ser. 4, vol. 3 (A) no. 1, pp. 3-23.
- Favorskaya, T. A. 1988, 'Bryozoans of the West Uzbekistan', *Byul. MOIP. Otd. geol.*, vol. 63 no. 1, pp. 64-102.
- Favorskaya, T. A. 1992, 'Bryozoans of the Campanian and of the Maastrichtian of the South and East of the USSR', *Tr. VSEGEI. St Petersburg. Nedra*, vol. 350, pp. 115-136.
- Gordon, D. P. 1989, 'The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomata, Ascophorina) from the Western South Island continental shelf and slope', *New Zealand Oceanogr. Inst. Mem.*, vol. 97, pp. 1-106.
- Hayward, P. J. & Ryland, J. S. 1979, *British ascophoran bryozoans — Synopsis of the British fauna*, Academic Press, New York, vol. 14 pp. 217-233.
- Keij, A. J. 1972, 'The bryozoan genus *Skylonia* Thomas (Cheilostomata)', *Bull. Brit. Mus. (Natur. Hist.) Geol.*, vol. 24 no. 3, pp. 217-233.
- Kluge, G. A. 1962, *Bryozoa of the North seas of the USSR, AN SSSR*, Leningrad, Moscow, pp. 1-584.
- Larwood, J. P. 1962, 'The morphology and systematics of some Cretaceous Cribrimorph Polyzoa (Pelmatorporina)', *Bull. Brit. Mus. (Natur. Hist.) Geol.*, vol. 6 no. 1, pp. 1-285.
- Lidgard, S., McKinney, F. K., & Taylor, P. D. 1993, 'Competition on clade replacement and history of cyclostome and cheilostome bryozoan diversity', *Paleobiolog.*, vol. 19 no. 3, pp. 352-371.
- Pitt, L. J. & Taylor, P. D. 1990, 'Cretaceous Bryozoa from the Faringdon Sponge Gravel (Aptian) of Oxfordshire', *Bull. Brit. Mus. (Natur. Hist.) Geol.*, vol. 46 no. 1, pp. 61-152.
- Ponomareva, L. D. 1987, Miocene Cyclostomida (bryozoans) of the Volyno-Podolii, Dep. in VINITI Archives, Moscow, File No. 4254-B87, pp. 1-198.
- Pouyet, S. 1965, 'Bryozoaires de l'Eocene et du Miocene de Syrie (Libye)', *Lab. Soc. Geol. France, Fasc.* 3, pp. 1-96.
- Ryland, J. S. & Hayward, P. J. 1977, *British anascan bryozoans — synopsis of the British fauna* vol. 10, Acad. Press, New York, pp. 1-188.
- Schaefer, P. & Fois, E. 1987, 'Systematics and evolution of Triassic Bryozoa', *Geologica and Paleontologica*, vol. 21, pp. 173-225.
- Taylor, P. D. 1986, 'Charixa Lang and Spinicharixa gen. nov., cheilostome bryozoans from the Lower Cretaceous', *Bull. Brit. Mus. (Natur. Hist.) Geol.*, vol. 40 no. 4, pp. 197-222.
- Taylor, P. D. 1994a, 'An early cheilostome bryozoan from the Upper Jurassic of Yemen', *N. Jb. Geol. Palaeontol. Abh.*, vol. 191 no. 3, pp. 331-344.
- Taylor, P. D. 1994b, 'Systematics of the meliceritid cyclostome bryozoans; introduction and the genera *Elea*, *Semielea* and *Reptomulteia*', *Bull. Natur. Hist. Mus. Lond. Geol.*, vol. 50 no. 1, pp. 1-104.
- Taylor, P. D. & Michalik, J. 1991, 'Cyclostome bryozoans from the Late Triassic (Rhaetian) of the West Carpathians, Czechoslovakia', *N. Jb. Geol. Palaeontol. Abh.*, vol. 182 no. 3, pp. 285-301.
- Vavra, N. 1977, *Bryozoa tertiaria: Catalogues fossilium Austriac.*, Oester. Acad. Wissenschaft, Wien, pp. 1-210.
- Viskova, L. A. 1972, 'Late Cretaceous cyclostomatous Bryozoa of the Volga River region and the Crimea', *Tr. Paleont. in-ta AN SSSR Moscow*, vol. 132, pp. 1-96.
- Viskova, L. A. 1980, 'Phylum Bryozoa', in *Developement and the change of the Invertebrata at the boundary of the Mesozoic and Cenozoic*, Nauka, AN SSSR, Moscow, pp. 4-21.
- Viskova, L. A. 1992, 'Marine post-Paleozoic Bryozoa', *Tr. Paleont. in-ta RAN, Moscow*, vol. 250, pp. 1-187.
- Viskova, L. A. & Morozova, I. P. 1993, 'Evolutionary changes of marine bryozoans and the critical situation in the Phanerozoic', *Paleont. Zhur.*, vol. 3, pp. 49-55.
- Voigt, E. 1967, 'Oberkreide-Bryozoen aus den asiatischen Gebietender UdSSR', *Mitt. Geol. Staatsinst. Hamburg*, vol. 36, pp. 5-95.
- Voigt, E. 1981, 'Repartition et utilisation stratigraphique des Bryozoaires de Cretace Moyen (Aptien-Coniacien)', *Cretaceous Research*, vol. 2, pp. 439-462.
- Voigt, E. 1985, 'The Bryozoa of the Cretaceous-Tertiary boundary', in *Bryozoa: Ordovician to Recent*, eds Claus Nielsen & Gilbert P. Larwood, Olsen & Olsen, Fredernborg, Denmark, pp. 329-342.
- Voigt, E. 1987, 'Die Bryozoen des klassischen Dano-Montiens von Mons (Belgien)', *Mem. Expl. Cartes. Geol. Mu. Belgique*, vol. 3 no. 17, pp. 1-161.
- Voigt, E. 1989, 'Beitrag zur Bryozoen-Fauna des Saschischen Cenomaniums. Revision von A. E. Reuss "Die Bryozoen des unteren Quaders" Teil. 1: Cheilostomata', *Abh. Staat. Mus. Mineral. Geol.*, vol. 36, pp. 8-87.
- Voigt, E. & Hillmer, G. 1983, 'Obercretazische Hippothoidae (Bryozoa Cheilostomata) aus dem Campanium von Schweden und dem Maastrichtium der Niederlande', *Mitt. Geol. Palaeontol. Inst. Univ. Hamburg*, vol. 54, pp. 169-208.
- Walter, B. 1969, 'Les Bryozoaires jurassiques en France', *Docum. Lab. Geol. Fac. Sci. Lyon*, no. 35, pp. 1-328.
- Weiss, O. B. 1988, 'Miocene bryozoans of the North Caucasus and the Crimea', *Tr. Paleont. in-ta AN SSSR, Moscow*, vol. 232, pp. 1-102.



## 1.6 Echinoids at the Cretaceous–Paleogene Boundary

A. V. Markov and A. N. Solovjev

### Introduction

This paper presents results of investigations on echinoid evolution at the Cretaceous/Paleogene boundary (Moskvin et al. 1980; Markov 1994; Markov et al. 1994; Moskvin 1989; Solovjev & Mironov 1991; Solovjev et al. 1994, 1995).

Many regions within the territory of the former USSR that have representatives of Late Cretaceous and Paleogene echinoid faunas belong to the European Province (Precarpathien, Donets Basin, Crimea, Caucasus, Mangyshlak, Western Turkmenia). The eastern part of Middle Asia belongs to the Mediterranean Province. Material of Late Cretaceous and Paleogene echinoids from Crimea, the Caucasus and the Transcaspian regions comes from excellent and continuous outcrops. Late Paleocene echinoid association is the most interesting owing to its completeness and diversity. There seems to be no other place in the world where Late Paleocene echinoids are so abundant and well preserved. Many echinoid groups were flourishing during the Late Cretaceous, especially during the Campanian and Maastrichtian.

Twenty-two percent of families and 50% of genera of regular echinoids and 33% of families, 67% of genera of irregular echinoids present in the Late Cretaceous had become extinct by the end of the Maastrichtian. The extinction of families and genera was occurring gradually through the Late Senonian.

The change of the species' composition at the Maastrichtian–Danian boundary seems to be rather sudden. More than 70 Maastrichtian echinoid species are known from the former USSR territory. None of them are found in the Danian.

Paleocene faunas form a peculiar association, which is less diverse than that of the Late Cretaceous (Maastrichtian). Fourteen percent of Paleocene families and 36% of genera are absent in the underlying beds. There are about 50 echinoid species in the Danian of the USSR. The Danian–Montian boundary is much more poorly defined and can be noticed at the species level only. The Montian–Thanetian boundary is more abrupt. Several new, peculiar genera and numerous species appeared in the Thanetian. Some of the typical Paleocene genera became extinct at the end of the Paleocene.

The modern phase (Cenozoic) of echinoid evolution really began in the Early Eocene. Thirty-two percent of Eocene families and 81% of genera are new.

The changes in marine communities at the Mesozoic–Cenozoic boundary involved not only the extinction of some groups and appearance of the others, but also their redistribution in different zones of the ocean. An excellent example is the development of the Order Holasteroida. The majority of holasteroid genera became extinct at the end of the Cretaceous, and more became extinct in the Paleocene. Holasteroids do not occur in post-Paleocene deposits anywhere except in Australia and New Zealand. They are nearly absent in the shelves of the recent seas, but they are widely distributed in bathyal and abyssal zones (Solovjev & Mironov 1991).

It is noteworthy also that the tests of Early Danian echinoid species in some regions (e.g. Crimea and Mangyshlak) are considerably smaller than the Late Maastrichtian species. This may be related either to worsening of conditions (climate cooling) or to the rapid eustatic lowering of the ocean level. As a result, the deep-water echinoid community was forced into shallower waters.

### Quantitative Analysis of Echinoid Extinction at the Mesozoic–Cenozoic Boundary

Today many scientists are inclined to think that mass extinctions, such as the extinction at the Mesozoic–Cenozoic boundary, were caused mainly by external (probably extra-terrestrial) factors (Alekseev 1984; Grunt 1992; Moskvin et al. 1980; Solovjev et al. 1994; McKinney et al. 1992; Raup & Sepkoski 1982). It is far more difficult to answer another question: why were different taxa influenced by external crises in such a different way?

Echinoid extinction at the Mesozoic–Cenozoic boundary was extremely selective. It is possible to understand several parameters connected directly or indirectly with the level of extinction in different echinoid taxa. They are: the age of the taxon (young, mature or old); the phase of evolutionary development of the taxon at the moment of the crisis (growth, acme or decline); specific morphological and ecological characters; the size of area inhabited by the taxon; the level of specialisation of genera and species.

### The Selectivity of Echinoid Genera Extinction in Dependence on Their Age

At the time of the Mesozoic–Cenozoic crisis the younger genera (those which had just appeared) died out on a larger scale. For example, among 19 genera of Regular echinoids whose age was less than 20 my. in the Maastrichtian, 10 genera (52.6%) did not cross the Maastrichtian–Danian boundary; among 14 genera aged

20–40 my. only two (14.3%) became extinct; among the 10 oldest genera (aged over 60 my.) three (30%) became extinct.

This relation between the extinction and age of genera is characteristic not only of this crisis but of other epochs as well (Markov et al. 1994). It has been shown that the survivorship curves of Regular and Irregular echinoid genera are exponential and can be divided into three parts characterised by different rates of extinction (Markov & Naimark 1994a). The probability of extinction is the highest in younger genera, the lowest in mature genera and medium in the oldest. The Mesozoic–Cenozoic boundary crisis increased proportionally the rates of extinction in the three age groups without changing the age structure of extinction. The changes in the probability of extinction of taxa in accordance with their age resemble the age-related changes with the probability of individual death. This is one of the facts that suggests the presence of systemic features in high taxa (Chernykh 1986).

#### Relation Between the Extinction Level and the Phase of Evolutionary Development

There was a regular succession of evolutionary phases in the development of various higher taxa (Markov & Naimark 1994b, 1994c, 1995). These phases are described in our first paper in this volume. The stability of genera depends to a large extent on the phase of development of the corresponding family (order). In irregular echinoids, the extinction level at the Mesozoic–Cenozoic boundary was much lower in genera that appeared in young families than in genera whose families were old at the moment of their origin. How can we explain this?

According to the model suggested by Markov and Naimark (1994c) during the first phases of evolution of a family, new genera are usually not specialised, tolerant or eurybiontic, because there is much vacant ecological space in the familial adaptive zone. When the family reaches its acme, the number of vacancies decreases and the competition between genera becomes stronger. As a result, the new genera usually are specialised, vulnerable and unstable. The extinction level at the Cretaceous–Paleogene boundary was higher in the taxa in the phases of acme and decline than in those in the phase of extensive divergence (growth). The order Holasteroida in the Senonian has passed from acme into decline. The new holasteroid genera during this epoch were mostly specialised, often endemic. Tolerant and widely distributed eurybiontic genera almost ceased to appear. As a result, only four holasteroid genera crossed the Cretaceous–Paleogene boundary. At the same time the situation in the order Spatangoida was quite different. Several spatangoid families during the Senonian were still in the phase of extensive divergence. Eurybiontic genera with large areas of distribution (*Linthia*, *Cyclaster*) appeared. In accordance with this, the level of extinction

in the spatangoids was lower: 14 genera out of 37 survived into the Paleocene.

To analyse separately the main spatangoid families may be even more convincing. There is a distinct relation between the average size of areas of genera that appeared during the Senonian and percentage of genera that have survived into the Paleocene (size of area is regarded as an estimation of generic tolerance, or euryoky). The size of area was measured with the help of geographical distribution index (GDI). GDI = 1 means that the genus was distributed only within one square with side length of 10 degrees by latitude and longitude; GDI = 3 when the genus is widely distributed in one large region, such as in Australia or North America; in cosmopolitan genera GDI = 30 (Markov & Naimark 1995).

During the Senonian, five new genera appeared in the family Cyclasteridae with average GDI = 1 conventional units (c.u.). Four genera out of five have survived the Paleocene. Five genera with average GDI = 4.4 c.u. appeared during the Senonian in the family Paleostomatidae; three genera out of six have crossed the Cretaceous–Paleogene boundary. Five new genera with average GDI = 2.6 c.u. appeared in the family Hemiasteridae; only four out of nine have survived into the Paleocene. Two new genera (average GDI = 2.0) appeared in the family Micrasteridae; the family had died out completely during the Maastrichtian.

#### Relation Between the Probability of Extinction and the Level of Specialisation

Apparently the degree of specialisation was the main factor that influenced the probability of extinction during the crisis. The degree of specialisation can be measured not only by expert estimations, but also by some indirect parameters, such as GDI. Echinoid genera that inhabited larger areas were usually more long-lived than genera with smaller areas. Average GDI in echinoid genera that became extinct in the Maastrichtian (or Senonian, if the moment of extinction is not determined more precisely) equals 5.6 c.u.; in genera that passed into the Cenozoic GDI = 11.5 c.u. (statistical significance of this difference exceeds 99.6%).

#### Relation Between the Probability of Extinction and Morphological and Ecological Characters

Extinction at the Cretaceous–Paleogene boundary was selective concerning genera with different morphology and ecology. First of all, it relates to the characters connected with the degree of euryoky. The genera that were able to tolerate various conditions appeared to survive better than the stenobiontic ones. This rule can be illustrated by the extinction patterns in the superorder Spatangacea. Genera of Spatangacea without fascioles are not able to burrow, so they cannot get food particles from the inner layers of the sediment. The extinction in these genera was greater than in those with fascioles (the latter



genera are capable of burrowing and can get food particles both from the surface of the sediment and from the deeper layers).

Another important feature is the frontal groove. Spatangaceans without a frontal groove collect food with the help of the adoral tubefect (feeding by means of collection). The frontal groove provides the ability of the second additional mode of feeding — suspension feeding. Suspended material is channelled onto the mucus string of the frontal groove. Mucus is secreted by the miliary spines in the adoral part of the groove. It moves adorally because of the action of these spines (Smith 1984). Sometimes when the groove is very deep, there can be a partial reduction of the adoral tubefect. Apparently these forms depend almost completely on the suspension feeding. Therefore, genera without a frontal groove, or that have a very deep groove, can be regarded as specialised (they use only one mode of feeding), while genera with a moderately developed groove are more eurybiontic (they can use both ways of feeding). Related to this, the extinction at the Cretaceous–Paleogene boundary was the largest in genera without a frontal groove, somewhat smaller in genera with a very deep groove; genera with a moderate groove were the least affected by the crisis.

Petals are used for respiration inside the sediment. They can be either flush with the surface of the test or more or less deeply sunken. The former type is excellent for burrowing into coarse-grained sediment only (stenobiontic forms), while the latter is good for any kind of sediment (eurybiontic forms). Accordingly, the generic diversity of Spatangacea without petals and with flat petals decreased greatly at the Cretaceous–Paleogene boundary, while the diversity of Spatangacea with sunken petals did not decrease at all.

## Conclusion

The major factor that determined the probability of an echinoid genus becoming extinct at the Cretaceous–Paleogene boundary was apparently the degree of specialisation. Stenobiontic genera became extinct, while eurybiontic ones passed to the Cenozoic. All the other relations discussed here are nothing but a number of different manifestations of this rule. The higher extinction rate in young (newly appeared) genera is explained by the fact that they had no time to diversify and to occupy all the area and resources potentially accessible to them (the number of species in younger genera is usually small). The relatively high vulnerability of old genera is connected with the fact that many 'aged' genera become too specialised (the typical example is *Micraster*). The higher extinction of genera in old families in the phases of acme and decline is explained by the fact that there are no vacancies left in the adaptive zone of the family, and new genera appear through division of niches, which is always accompanied by specialisation. The high vulnerability of genera with small geographic areas is related to that limited

geographical distribution which is characteristic of specialised taxa. Finally, the analysis of the relation between the extinction and morphology shows that genera which are able to exist only in a limited range of conditions are always more vulnerable than the eurybiontic genera.

## References

- Alekseev, A. S. 1984. 'Quantitative analysis of Mesozoic/Cenozoic boundary extinction'. *Bull. Moscow soc. of naturalists. Geol.*, vol. 59 no. 2, pp. 87–102 (in Russian).
- Chernykh, V. V. 1986. *Problem of integrity of high toxo*, Nauka, Moscow, p. 142.
- Grunt, W. 1992. *Evolutionary process*, Mir, Moscow, p. 488 (in Russian).
- McKinney, M. L., McNamara, K. J., Carter, B. D., Donovan, S. K. 1992. *Evolution of Paleogene Echinoids: a global and regional view. Eocene–Oligocene and Biotic Evolution*, Princeton Univ. Publ., pp. 349–367.
- Markov, A. V. 1994. 'Morphology, systematics and phylogeny of schizasterid sea urchins', *Transactions of the Paleontol. Inst. Russian Acad. Sci.*, vol. 258, p. 94 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994a. 'Survivorship curves as a proof of reality of supraspecific taxa', *Paleontol. J.*, no. 2, pp. 3–11 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994b. 'The dynamics of phylogenetic processes in supraspecific biosystems', *Paleontol. J.*, no. 3, pp. 3–12 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994c. 'A study of a high taxon diversity dynamics by means of mathematic modelling', *Jour. General Biology*, no. 3, pp. 303–31 (in Russian).
- Markov, A. V. & Naimark, E. B. 1995. 'Connection of the level of diversity of higher taxa with the degree of specialisation of genera and species (illustrated by certain groups of paleozoic invertebrates)', *Jour. General Biology*, no. 1, pp. 97–107 (in Russian).
- Markov, A. V., Naimark, E. B. & Solovjev, A. N. 1994. 'Selective extinction of the sea urchins in crisis epochs dependently on age of the taxa', *Jour. General Biology* no. 2, pp. 171–178 (in Russian).
- Moskvin, M. M. 1989. *Echinoids of the Mesozoic–Cenozoic boundary beds. Fossil and recent echinoderm researches*, Tallinn, pp. 175–188 (in Russian).
- Moskvin, M. M., Solovjev, A. N. & Endelman, L. G. 1980. *Echinoids. Development and change of invertebrates at the Mesozoic/Cenozoic boundary*, Nauka, Moscow, pp. 116–167 (in Russian).
- Raup, D. M. & Sepkoski, J. J. 1982. 'Mass extinctions in the marine fossil record', *Science*, vol. 215 no. 4539, pp. 1501–1503.
- Smith, A. 1984. *Echinoid Palaeobiology*, George Allen and Unwin, London, p. 190.
- Solovjev, A. N. & Mironov, A. N. 1991. *History of the formation of the deep-sea echinoderm fauna. Major biological events in Earth history* (Transactions of the XXXII session of All-Union Paleont. Soc.), Tallinn, pp. 135–142 (in Russian).
- Solovjev, A. N., Viskova, L. A., Markov, A. V., Shimansky, V. N. 1995. 'Pre-history of the marine biota crisis at the Cretaceous–Tertiary boundary (Cephalopoda, Bryozoa, Echinoidea)', *Bull. Moscow soc. of Naturalists. Geol.*, vol. 70 no. 1, pp. 49–61 (in Russian).
- Solovjev, A. N., Viskova, L. A., Markov, A. V., Shimansky, V. N., Naimark, E. B. 1994. *Changes in the marine biota at the Mesozoic–Cenozoic boundary. Ecosystem restructures and the evolution of biosphere*, Nedra, Moscow, pp. 151–160 (in Russian).





## 1.7 The Quantitative Analysis of Echinoid Evolution

A. V. Markov and A. N. Solovjev

Numerous factors show that higher taxa evolve as integrated systems, and not as sets of independent species (Chernykh 1986). The quantitative analysis of echinoid evolution makes it possible to find the manifestations of systemic properties in many echinoid taxa. The survivorship curves of echinoid genera, as well as Irregular echinoid families, are exponential (Markov & Naimark 1994a). This means that the extinction of the supraspecific taxa can be described by the same relationships as the disintegration or collapse of the other integrated systems. It is interesting that when we take random sets of species instead of natural genera, the survivorship curve ceases to be exponential. The survivorship curves of natural taxa usually consist of three parts with slightly different coefficients: the probability of extinction is usually higher in a young (recently originated) taxon than in a 'mature' one. As the mature taxon grows older, its vulnerability increases again. The pattern is very similar to the age-related changes in the probability of the organism's death (Tjurin 1972).

The systemic properties of the supraspecific taxa can be observed in the regular dynamics of various quantitative parameters (level of diversity, tempo of extinction and origination of sub-units) during the evolution of the 'average echinoid family' (Markov & Naimark 1994b). The diversity dynamics in the average echinoid family is usually described by a domed curve; the rate of generic origination decreases; the rate of generic extinction increases.

These and other quantitative tests have shown that the systemic properties are clearly manifested in the majority of echinoid genera and in the Irregular echinoid families; much less so in the Regular echinoid families. Probably the systemic properties of the supraspecific taxa reflect the degree of their ecological specificity. For instance, the specific morphological and functional characters of Family A make it possible to occupy some particular adaptive zone, which is different from the zone occupied by Family B. Thus, the term 'taxon' may completely or partially be the same as the term 'life form'. In other words, the integrity of a taxon may be related to the presence of an integrated adaptive zone. Probably, the weak manifestation of systemic properties in Regular echinoid families is connected with the fact that the borders of their adaptive zones are somewhat obscure (they are usually strongly overlapping). Evidently Regular echinoid families differ ecologically from one another to a much smaller extent than the Irregular echinoid families. The other possible reason is the incompleteness of the Regular echinoid fossil record (Kier 1977). This incompleteness makes our calculations of diversity and the time of origination and extinction much less precise than in Irregular echinoids.

In order to explain the quantitative regularities found in the development of higher taxa, a simulation computer model has been elaborated (Markov & Naimark 1994c). In this model a higher taxon (family) evolves within a strictly limited region of the resource space (the adaptive zone). The family consists of genera. Each genus occupies a certain part of the familial adaptive zone. The volume of the resource space occupied by the genus reflects the level of its euryoky (tolerance). If this volume is small, then the genus is specialised (stenoeceic); if it is large, then the genus is not specialised (euryoeceic, or tolerant). Each genus can produce new genera in two different ways:

1. Extensive divergence (new genus occupies some vacant part of the familial adaptive zone);
2. Intensive divergence (the adaptive zone of the ancestor genus splits in two).

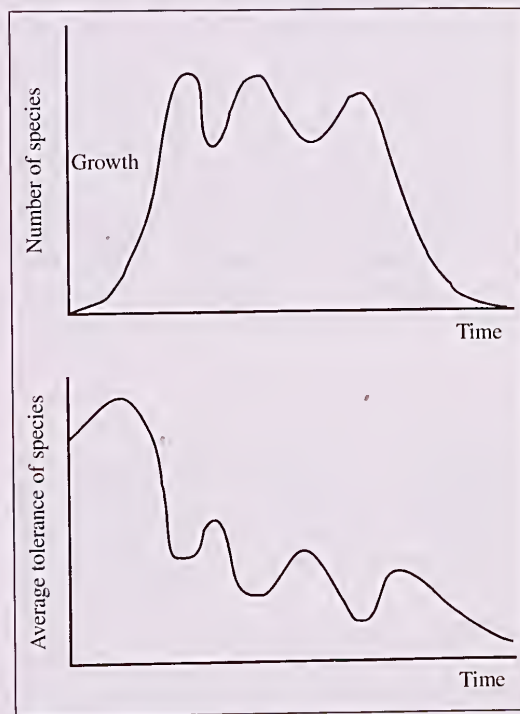


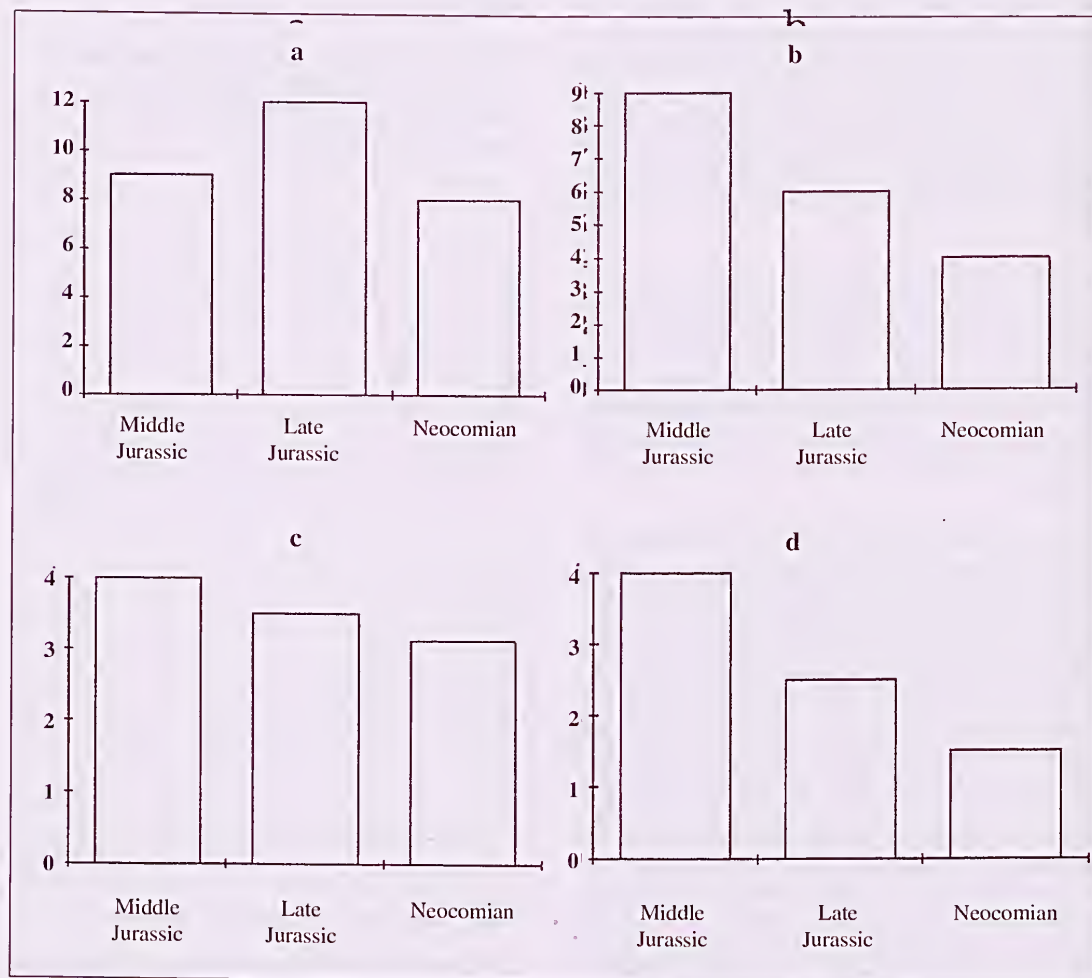
Figure 1 Development of a taxon in the simulation model.

The probability of extensive divergence is higher when there is much vacant space in the familial adaptive zone and when the ancestor genus is euryoeceic. The probability of intensive divergence, on the contrary, becomes higher when the volume of the vacant space in the familial adaptive zone decreases. The probability of extinction is higher in the stenoeceic genera (the rule of the selective extinction of specialised taxa). The evolution of the family

in the model consists of three phases (fig. 1). The same phase can be easily determined in the evolution of many real echinoid taxa. The phases are as follows:

1. Phase of extensive divergence. There is plenty of vacant space in the familial adaptive zone. The probability of extensive divergence is high. The new genera are usually tolerant. In real taxa the symptoms of this phase are: the origination of widely distributed, long-lived and euryoecic taxa; the increase of generic diversity; high tolerance of the taxon to environmental change;

2. Phase of acme (climax). There is almost no vacant space left in the familial adaptive zone. The probability of extensive divergence is low; the probability of intensive divergence is high. The average level of generic specialisation grows rapidly. In real taxa (as well as in the model) the most spectacular symptom of the phase is counter-phase fluctuations of generic diversity and the average level of generic euryoky. It means that during the periods of mass origination the new genera are usually specialised, so that the average level of euryoky in the family decreases. During the periods of extinction this level increases, because the specialised genera are always more likely to become extinct than the euryoecic genera;



**Figure 2** Quantitative parameters in the evolution of the Disasterid Echinoids (families Disasteridae and Collyritidae):

- Total number of genera;
- Number of new genera (first occurrence in the epoch);
- Average geographical distribution index (area size) of the genera;
- Average geographical distribution index of the new genera.



3. Phase of decline. Genera become so specialised, that they begin to lose the ability to occupy the niches that have been vacated by the extinct genera. The generic diversity decreases. The new genera originate only through intensive divergence, or there are no new genera at all.

The typical succession of the evolutionary phases can be found, for instance, in the evolution of the disasterid echinoids (families Disasteridae and Collyritidae) (Solovjev 1971). This group appeared in the Middle Jurassic and became extinct in the Early Cretaceous (fig. 2). During the Middle Jurassic the group was in the phase of extensive divergence; the generic diversity was increasing, the new genera were comparatively long-lived and widely distributed. During the Late Jurassic the group was in the phase of acme: the tempo of generic origination decreased, the generic diversity ceased to grow, the new genera were short-lived and mostly endemic. It is very spectacular that all the Jurassic genera that crossed the Jurassic–Cretaceous boundary had originated during the Middle Jurassic, not during the Late Jurassic. In the Neocomian the group was in the phase of decline: the generic diversity decreased, all the new genera were short-lived and endemic.

The first representatives of many large echinoid taxa were inadaptable groups (the terms 'inadaptation' and 'euadaptation' have been defined by Rasnitsyn (1986). The typical example is the group mentioned above, the disasterid echinoids, the most ancient representatives of the superorder Spatangacea. Their quickly attained, but not well-balanced and rather limited, morphological adaptations gave an opportunity to occupy some niches in the adaptive zone of the soft sediments. This can be seen from the main life forms of the Jurassic spatangaceans. These life forms were repeatedly 'copied' afterwards by the Cretaceous and Cenozoic representatives of the superorder on a much higher level of organisation.

According to the model described, a specialised taxon usually becomes extinct without leaving any descendants. Still, sometimes the specialised forms can produce new large taxa. This is possible when the adaptive zone of the taxon has contacts with the vacant regions of the resource space. In this case, a specialised genus in the marginal part of the familial adaptive zone has good chances to attain the 'preadaptations' for moving into these vacant regions. For instance, at the beginning of the Cretaceous the disasterid echinoids (the group was in the phase of decline) gave rise to the advanced and euadaptive families Holasteridae and Toxasteridae. At the end of the Cretaceous the order Holasteroida was in the phase of decline; yet at this time the first representatives of the deep sea families Pourtalesiidae and Urechinidae appeared. Probably, the mechanism of occupying a new region of the resource space was similar in both cases. The transfer was accomplished by rather specialised forms (probably some despecialisation took place as well) which were inhabiting the marginal parts of the adaptive

zone of a higher taxon (these parts must have been in contact with some vacant regions of the resource space). This hypothesis helps to explain why the occupation of a new adaptive zone in the evolution of the holasteroids and spatangoids often took place only after the vacancies in the old adaptive zone had been exhausted. While there are still enough vacancies in the old adaptive zone, the competition between genera is low, and there are no reasons for specialisation.

The taxa of the same rank usually differ in the duration of the phylogenetic phases. These differences may be connected with different location of the adaptive zones of the taxa in the resource space. This idea can be illustrated by the evolution of the orders Spatangoida and Holasteroida during the Cretaceous. At the beginning of the Cretaceous both orders (except for the disasterid echinoids) were in the phase of extensive divergence. In the middle of the Cretaceous the holasteroids were in the phase of acme; at the end of the period they were in the phase of decline. In the majority of spatangoid families the extensive divergence went on to the end of the Cretaceous. This difference was probably due to the more advantageous location of the adaptive zone of the first real spatangoids (family Toxasteridae) in the resource space compared to the adaptive zone of the holasteroids (family Holasteridae). The 'advantageous location' means that their adaptive zone was in contact with vast vacant regions of the resource space. The holasteroids were mostly epibenthic or partially burrowing; therefore, their evolutionary capabilities were limited by the strong competition with other echinoid orders. The spatangoids were able to burrow completely in the sediment (sometimes to a considerable depth); this aided them in avoiding competition, so that they could occupy a vast, vacant region of the resource space without serious obstacles.

## Conclusion

The similar succession of phases in the evolution of different echinoid taxa demonstrates that the evolutionary pattern of a taxon depends not only upon the fluctuations of environment, but also on the properties of the group itself, such as the size of the adaptive zone and its location in the resource space.

The quantitative analysis of the echinoid evolution supports the idea of the supraspecific taxa evolving as integrated systems. Thus, when studying the quantitative aspects of macroevolution it seems reasonable to apply a model, according to which each taxon evolves within the borders of the adaptive zone of some limited size. Various quantitative evolutionary patterns depend upon the volume of the vacant ecological space left in the adaptive zone. These facts correspond to the ideas of Schwartz (1980), who wrote that the origination of a new taxon is to some extent similar to the occupation of an isolated island. At the early stage of the taxon's evolution a rapid diversification usually takes place; the most ancient

clades are likely to be inadapative. This is manifested, for instance, in the fact that the ancient representatives of the taxon sometimes differ from one another on a specific level by characters which later will become generic or familial (the rule of archaic diversity).

## References

- Chernykh, V. V. 1986, *The problem of the integrity of high taxa*, Nauka, Moscow, p. 142 (in Russian).
- Kier, P. M. 1977, 'The poor fossil record of the Regular Echinoids', *Paleobiology*, no. 3, pp. 168-174.
- Markov, A. V. & Naimark, E. B. 1994a, 'Survivorship curves as a proof of the reality of supraspecific taxa', *Paleontol. J.*, no. 2, pp. 3-11 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994b, 'The dynamics of phylogenetic processes in supraspecific biosystems', *Paleontol. J.*, no. 3, pp. 3-12 (in Russian).
- Markov, A. V. & Naimark, E. B. 1994c, 'The study of diversity dynamics in high taxa by means of mathematic modelling', *Jour. General Biology*, no. 3, pp. 303-317 (in Russian).
- Markov, A. V., Naimark, E. B., & Solovjev, A. N. 1994, 'Selective extinction of the sea urchins in crisis epochs dependently on age of the taxa', *Jour. General Biology*, no. 2, pp. 171-178 (in Russian).
- Rasnitsyn, A. P. 1986, 'Inadaptation and euadaptation', *Paleontol. J.*, no. 1, pp. 3-7 (in Russian).
- Schwartz, S. S. 1980, *Ecological patterns of the evolution*, Nauka, Moscow, p. 278 (in Russian).
- Solovjev, A. N. 1971, 'Late Jurassic and Early Cretaceous disasterid Echinoids of the USSR', *Transactions of the Palaeontological Institute of the Academy of Sciences of the USSR*, vol. 131, p. 124 (in Russian).
- Tjurin, P. V. 1972, '"Normal" curves of surviving and of the tempo of natural mortality of fish as a theoretical base of the fisheries management', *Transactions of the State Inst. of Oceanography and Fisheries*, vol. 71, p. 81 (in Russian).



## 1.8 Biocenotic Preconditions for the Advent of Vertebrates onto Land, and the Position of the Terrestrial Tetrapod Community in the Biosphere of Earth

A. S. Rautian

### Physiological Limitations of Amphibian Organisation

**Pulmonary breathing as an addition to the main, branchiate adaptation, was achieved in the primary aquatic ancestors of tetrapods, Rhipidistia** (Tatarinov 1972; Carroll 1988). Pulmonary breathing in amphibians constitutes not more than 40% of general oxygen metabolism (Tatarinov 1959, 1960). The absence of definitive gills in an amphibian was compensated for by intensified skin breathing, which became dominant. In lungless salamanders (Plethodontidae), among which there are many terrestrial forms, pulmonary breathing is easily reduced and skin breathing predominates.

**Prohibitions on division of venous and arterial blood circulation in pulmonate Anamnia.** A three-chambered heart and mixed blood circulation arose in connection with the emergence of pulmonary breathing and were also inherited by amphibians from Rhipidistia. However, the role of blood mixing amplifies in amphibians: due to this the blood is enriched with oxygen, over that which flows in the venous vessels from skin to the heart and can enter into the arterial system (Tatarinov 1959, 1960). Thus, the prohibition on division of venous and arterial currents of blood arises in Anamnia in the conditions of pulmonary breathing. In amphibians it becomes even more important in comparison with their primary aquatic ancestors.

**Reinforcement of a passive respiratory function of skin** was achieved at the price of:

1. Thermal cooling of body in air environment because of evaporation from the surface of moist skin, which prevented the use of not only internal (prohibition on any form of warm-bloodedness), but external warmth, as well;
2. Prohibition on formation of economical water exchange and independence from water aquatic environments;
3. Reduction of efficiency of protective functions of skin.

These features were not fully attained (Rautian 1988) in amphibians, and in particular, were the causes of the advantage that reptiles had not only on land, but also in the sea (Kalandadze & Rautian 1994).

**Topographical overlap of the organs of gular breathing and feeding in amphibians** prevents the optimisation of both jaw apparatus and pulmonary breathing. A flat wide skull, framed along the lower outside edge by a mandible, provides a significant increase of the volume of the mouth-and-throat (gular) cavity in the process of separation of its base from the

palate; but it limits the number of designs possible for the skull; hindering, in particular, the possibility of upright position of jaw muscles (Rautian 1988); i.e. their positioning in the plane on mandibular movements. Gular breathing requires the uncompromising division of the cavity of the adductor muscles and the gulars. Thus, the only location for attachment of the adductors of the mandible is near the jaw joint. This limits the force generated by the jaw muscles considerably, although it promotes a wide opening of the mouth.

Additionally, gular breathing hinders a long period of processing of food in the mouth, and prohibits isolation of breathing from the mouth cavity with the help of the secondary palate, thus lowering the efficiency and speed of food digestion.

**Prohibitions on phytophagy in amphibians.** The thermal cooling, low efficiency of food procuring, primary processing of meal in the mouth and digesting, as well as gas and water exchange — all these limit the intensity of amphibian metabolism. All these amphibian parameters are inferior to those of the majority of fish and Amniota (Semalgaugen 1964, 1983; Prosser 1973; Schmidt-Nielsen 1979). Low efficiency of interchange of gases is confirmed indirectly by the comparatively large weight of white muscles in modern amphibians; these muscles 'tire' easily with heavy loading, but are capable of efficient short-term activity, even in conditions of oxygen shortage (Prosser 1973). For these reasons passive hunting is typical of amphibians; they wait for victims in ambush (they implement a living form of a 'live trap'); but they are incapable of hunting by using long-term pursuits of their victims.

The greatest mass, both widespread and accessible, both with low-calorie content vegetable foods are capable of supplying the necessary energy only in the case of a high rate of consumption and digestion. Both of these features are proportional to the intensity of metabolism. Therefore, there are no specialised phytophagous animals among amphibians and their primary aquatic ancestors with skin-and-lung breathing.

**Phytophagy is typical only of aquatic gill-breathing larvae** of ecaudate amphibians (Anura) and, probably, was their initial food specialisation (Semalgaugen 1964; Severtsov 1980, 1990). The thermal cooling, taking place in the open air environment, does not threaten them, neither does the mixture of venous and arterial blood currents. Tadpoles breath with gills, have a two-chambered heart with no mixing of the blood circulation, i.e. they possess a more efficient metabolism than does the adult form they give rise to with their skin-and-lung breathing.



## **Biocenotic Conditions for Advent of Vertebrates Onto the Land**

The restrictions on phytophagy in amphibians with their skin-and-lung breathing system, as well as in their direct phylogenetic ancestors, Rhipidistia, with a blood-mixing circulation (Tatarinov 1959, 1960), makes the mastering of land by vertebrates dependent on terrestrial colonisation by invertebrates so they can be utilised as food by ancient amphibians (Gilyarov 1949, 1970; Rodendorf 1970; Tatarinov 1972).

However, availability of a resident community of terrestrial invertebrates (bearing in mind that only such a community was able to feed ancient amphibians with low efficiency of food utilisation) is not only a requirement but also a considerable obstacle for the further advent of vertebrates onto the land. Terrestrial predators (such as large Chelicerata and Miriopoda of the Devonian) were a significant danger to the vertebrates deficient in specific adaptations to the terrestrial life. Hence, the mastering of land could be fulfilled only by vertebrates already having certain advantages in comparison with terrestrial invertebrates. Such an advantage, obviously, could have been the superiority of terrestrial vertebrates in size.

## **The position of Terrestrial Tetrapods in the Biosphere of the Earth**

**Fundamental limitation of sizes in terrestrial invertebrates** (Gilyarov 1949, 1970; Haldane 1976) was an important prerequisite of the advent of vertebrates onto the land.

**Vertebrates — the largest animals of the land.** Vertebrates differ from invertebrates in the absence of severe physiological limitations on sizes in terrestrial conditions. The internal skeleton does not hinder the optimisation of skin breathing. Increasing body sizes does not lead to such a great growth of skeleton weight as in the case of an external skeleton. Even amphibians possess active ventilation of lungs, which is amplified in comparison with Sarcopterygii due to the loss of gills. The latter has facilitated emergence of a hermetically sealed gular cavity. Owing to the lungs (which are inside the body, have a huge surface area, and are fixed in position), the circulatory system in vertebrates is capable of providing interchange of gases in a large body with small relative surface area of skin.

Advanced biomechanical theory about the origin of locomotion of terrestrial vertebrates was developed by Gambaryan (1990). It is based on expressed inertial properties of the animal body, which is not compatible with small size. The same can possibly be said in relation to the transformation of limb girdles during the adaptation of vertebrates to life on the land. It is difficult to find the sufficient adaptive basis for explanation of such transformations in a small-sized animal.

The large size of an animal (all other things being equal) increases the efficiency of the use of resources and reduces the loss of warmth on a unit of body weight in comparison with a small-sized animal (Slonim 1971; Rakhimov & Slonim 1981; Schmidt-Nielsen 1979). Therefore, the absence of prohibitions on large sizes is equal to preadaptation to their acquisition that we can establish as a tendency of increasing size during phylogenesis, which is peculiar to the majority of large taxa of tetrapods (one of Cope's rules).

Even very small tetrapods are larger than the majority of terrestrial invertebrates. This fact hints that the superiority in size over other terrestrial animals was likely an element in the strategy of ecogenesis of tetrapods during the whole phylogenesis of the group. Due to the superiority in size, ancestors of tetrapods were able to invade land previously inhabited by invertebrates. Moreover, no later than the Carboniferous their descendants succeeded in pushing out the largest terrestrial chelicerates (Krivolutskii 1978), myriapods and insects (Rodendorf 1970); increasing to even greater sizes and widening the gap between terrestrial vertebrates and invertebrates.

The peculiar role of the largest terrestrial animals that have trophic relations (mainly exchange of energy), but not competitive dependence (mainly regulatory) with the other components of biota is the most typical feature of ecology and ecogenesis of tetrapods, which made possible a considerable 'sovereignty' of their communities in terrestrial biocenoses.

Herbivorous and non-parasitic invertebrates are limited in numerous features by the capacity of energetic (trophic) input of the community of terrestrial tetrapods. This 'energy' grew slowly but surely in accordance with the development of plant resources and the growth of trophic specialisations in the processes of the phylogenesis of tetrapods.

The distribution (canalisation) of the input resources of the community of terrestrial tetrapods, depends mainly on ecological relations between the community members. In fact, the larger the animal, the lower the probability of its stenophagy (all other factors being equal): the strict limits of the food spectrum would make impossible the feeding of a population of sufficient numbers of large animals. It particularly concerns the low-caloric vegetable food, that should be consumed in large amounts by a phytophagous animal. Euryphagy of the tetrapods decreases specificity of their trophic connections with different species of plants and invertebrates.

**Tetrapods are the community of collectors of the standing crop, produced by terrestrial biocenoses.** Terrestrial tetrapods, first of all due to the superiority in size over other terrestrial animals, appeared not to be so much the components of particular (separate) biocenoses, subject to their strong regulatory effects, but a type of community, the guild of collectors of the standing crop

produced by biocenoses (usually by several, frequently many, sometimes very many biocenoses). Relatively large sizes of individuals does not permit the majority of populations of tetrapod species to limit themselves by only one particular biocenosis, the latter being limited by the corresponding phytoecoenosis. So, a population of a tetrapod species usually appears to be a member of several different biocenoses. Undoubtedly, the amount of stability of the standing crop influences the conditions of collectors, but efficiency of the use of the crop is determined first of all by the structure of consumption existing in the community of collectors themselves.

**Ecological functions of man in the biosphere of the Earth** is an extremely hypertrophied realisation of the main ecological strategy of tetrapods as collectors of crops, produced by the biosphere of the Earth, its natural and anthropogenic biocenosis. Being dissatisfied with the quantitative and qualitative range of natural crops, humans developed agriculture, that according to Vernadskii (1994) has led to 'autotrophy' of man. In fact, biomass of humanity exceeds tremendously that of any conceivable regular consumer. It became possible due to the emergence of agroecoses and the consumption of diverse resources, including irreplaceable mineral and mineralised resources of the biosphere. Man transformed himself into a sort of superconsumer.

However, continuous exhaustion of natural resources, some irreplaceable, testifies to:

1. Imperfect, ruinous character and incomplete autotrophy of a modern producing economy. As before, man, as well as other tetrapods, collects the crop; however, unlike other animals, he collects the crops not only of the modern biosphere, but also of the previous stages of biosphere development;
2. Consumer strategy of mankind as a whole is not much interested in sparing a particular producer (that is, finally, the biocenosis);
3. Very weak regulatory dependence on conditions of every particular biocenosis (after its exhaustion it is possible to pass over to exploitation of the next one).

On the other hand, man is totally dependent on the crop of the whole biosphere, which consists of biocenoses. The contradiction is that decomposing one biocenosis after another humans are gradually disturbing the biosphere, the very source of their well-being. Prerequisites of this contradiction, as has been pointed out, was contained in the main ecological strategy of terrestrial vertebrates, from the very moment of their advent on the land.

Thus, the origin of man as a part of the community of terrestrial tetrapods is an absolutely unusual event from the ecological and ecogenetical point of view. It had been prepared by all the previous phylogenesis of tetrapods and by phyloecoenogenesis of their community. The

development of these processes was made possible when vertebrates began to master the land as the largest terrestrial animals.

## References

- Carroll, R. 1988, *Vertebrate Paleontology and Evolution*, Freeman & Company, New York, p. 698.
- Gambaryan, I. S. 1990, *The factors of evolution of locomotory system of the lower tetrapods*, *Morfologiya mlekopitayushchikh i problemy lokomotsii* (Mammal morphology and the problems of locomotion), (Proc. Zool. Inst., AS USSR, vol. 215), ZIN AN SSSR Leningrad, pp. 9-37, (in Russian).
- Gilyarov, M. S. 1949, *Osobennosti pochvy kak sredy ovitaniya i ee znachenie v evolyutsii nasekomykh* (Peculiarities of soil the environment and its significance in the evolution of insects), AN SSSR, Leningrad, Moscow, pp. 279, (in Russian).
- Gilyarov, M. S. 1970, *Zakonomernosti prispособleniya chlenistonogikh k zhizni na sushe* (The rules of adaptation of arthropods to the life on land), Nauka, Moscow, pp. 276, (in Russian).
- Haldane, J. B. S. 1976, 'About expediency of size', in *John Bernard Sanderson Haldane: 1892-1964*, ed. G. E. Feldman, Nauka, Moscow, pp. 191-195.
- Kalandadze, N. N. & Rautian, A. S. 1994, *Conjugated evolution of terrestrial and aquatic tetrapods of the end of the Paleozoic and beginnings of the Mesozoic*, *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecosystem reorganisations and evolution of the biosphere), Nedra, Moscow, vol. 1, pp. 174-180, (in Russian).
- Krivolutskii, D. A. 1978, 'The ecological preconditions of advent of vertebrates onto the land', *Priroda*, no. 5, pp. 100-101.
- Prosser, C. L. (ed.) 1973, *Comparative Animal Physiology*, W. E. Saunders Co., Philadelphia-London-Toronto, p. 428.
- Rautian, A. S. 1988, 'Paleontology as the source of information about the laws and factors of evolution', *Sovremennaya paleontologiya* (Modern Paleontology), vol. 2, pp. 76-118.
- Rakhimov, K. R. & Slonim, A. D. 1981, *Ecological and physiological peculiarities of feeding, food obtaining and digestion*, *Rukovodstvo po fiziologii: Ecologicheskaya fiziologiya zhivotnykh*, ch. 2. *Fiziologicheskie sistemy v protsesse adaptatsii i faktory sredy obitaniya* (Manual on physiology: Ecological physiology of animals. Chap. 2. Physiological systems in the process of adaptation and the factors of environment), Nauka, Leningrad, pp. 408-465, (in Russian).
- Rodendorf, B. B. 1970, 'The significance of insects in the historical development of vertebrates', *Paleon. J.*, no. 1, pp. 10-18.
- Schmidt-Nielsen, K. 1979, *Animal Physiology: Adaptation and environment*, Cambridge Univ. Press, Cambridge, Eng., New York.
- Severtsov, A. S. 1980, *The evolution of mechanisms of food gripping and breathing in amphibians*, *Urovni organizatsii biologicheskikh sistem* (The levels of organisation of biological systems), Nauka, Moscow, pp. 49-75, (in Russian).
- Severtsov, A. S. 1990, *Napravlennost' evolyutsii* (The directionality of evolution), Mosk. Gos. Univ. Moscow, pp. 272, (in Russian).
- Shmalgauzen, I. I. 1964, *Proiskhozhdenie nazemykh pozvonochnykh* (The origin of terrestrial vertebrates), Nauka, Moscow, pp. 271, (in Russian).
- Shmalgauzen, I. I. 1983, *Puti i zakonomernosti evolyutsionnoy protsessy: Izbrannye trudy* (The routes and laws of evolutionary process: Selected works), Nauka, Moscow, pp. 360.
- Slonim, A. D. 1971, *Ecologicheskaya fiziologiya zhivotnykh* (Ecological physiology of animals), Vysshaya shkola, Moscow, pp. 448, (in Russian).
- Tatarinov, L. P. 1959 'The origin of reptiles and some principles of their classifications', *Paleon. J.*, no. 4, pp. 65-84, (in Russian).
- Tatarinov, L. P. 1960 'The evolution of apparatus of blood separation in the heart of vertebrates', *Zool. Zh.*, vol. 39, pp. 1218-1231, (in Russian).
- Tatarinov, L. P. 1972, *The ecological factors of origin of amphibians*, *Problemy evolyutsii* (The Problems of evolution), Nauka, Novosibirsk, pp. 144-153, (in Russian).
- Vernadskii, V. I. 1994, *Zhivoe veshchestvo i biosfera* (Alive substance and the biosphere), Nauka, Moscow, 671 pp. (in Russian).







# Crises and Their Symptoms

2





## 2.1 Symptoms of Ecological Crises

A. S. Rautian

We live in an epoch of progressively developing anthropogenic ecological crisis, menacing not only to civilization but the entire Earth's biosphere. The only experience at humanity's disposal is the experience of history. Therefore, as a whole, the construction of history of the biosphere based on the material from the geological record can not be underestimated.

An important step in this reconstruction is examination of the symptoms of ecological crises that constitute such a syndrome (Fedonkin 1991) – of the general characteristics of the crisis processes in the Earth's biosphere. The symptoms listed below were formulated against a background of results of study of two large, but different, ecological crises in the geological past.

The first of them was the global crisis of terrestrial and freshwater biocenoses in the middle Cretaceous investigated by the researchers in the Laboratory of Arthropods at the Palaeontological Institute, RAS. Thorough study was made of the insects, but also the involvement of the other components of the biota, i.e. the higher plants (Meien 1987; Vakhrameev 1988), other groups of terrestrial invertebrates (bivalves and gastropods, some crayfish, Chelicerata, etc.), and vertebrates (fish, amphibians, reptiles, birds and mammals) (Zherikhin 1979). At least in the case of insects and higher plants the crisis was the greatest in all of the subsequent history of the biosphere. The reaction of vertebrates was considerably weaker (Kalandadze & Rautian 1983, 1993a). The data on this crisis allowed Zherikhin (1978, 1979, 1987) to formulate the concept of biocenotic regulation of phylogenesis. He directed his main attention to the regulating effect of the structure of adaptive zones and ecological niches of a community of organisms, formed during the extended process of phylogenesis and having a steady repetition, onto the processes of phylogenesis of taxa constituting the biota of the community (Rautian 1993). According to this concept the degradation of community structure provokes an ecological crisis (Rasnitsyn 1988, 1989).

The second crisis studied by the authors (Kalandadze & Rautian 1983, 1993a) was the largest global crisis in the community of terrestrial (non-marine) tetrapods and took place in the Early and Middle Jurassic. Contrary to the crisis in the Cretaceous, this one was not accompanied by an appreciable crisis in other components of terrestrial biota, particularly in vegetation. The duration of its apogee was considerably longer than that of the crisis in the Middle Cretaceous. Independently of our study, this crisis has been noted by Benton (1985, 1987, 1988); but, he did not make an attempt to interpret its essential features. The data on this crisis allowed us to conclude the following:

1. The notion of significant autonomy of a community of terrestrial tetrapods, which appeared to be not only the components of a certain biocenosis, but the community of collectors of crops produced by several, sometimes by very many, biocenoses. Historically humans developed from a community of terrestrial tetrapods, with the same ecological strategy, but in extremely hypertrophied form. Man appears to be a sort of superconsumer of every possible resource, including irreplaceable mineral resources of the Earth. This is the ecological strategy of a consumer not so much interested in preservation of a particular producer (which is in the end the biocenosis itself), in combination with comparatively weak dependence on the condition of each particular biocenosis, (which, after being exhausted, could be left for the next one), has caused the extremes of the conflict between humans and the biosphere;
2. A heuristic model of the evolution of community structure and its biodiversity (its taxonomic and ecological diversity). The model is complementary to the concept of Zherikhin, to which it adds a mechanism of feedback, thus showing the role of processes of phylogenesis in structure formation and destruction during crises and restoration of the structure of community, its adaptive zones and ecological niches after crises.

Considerable distinctions of these two large ecological crises are obvious. The first one covers biocenoses of land as a whole, although not all their components to an equal degree. The second one affects selectively all the components of only one (a large one) group of organisms with considerable autonomy and specific function in the economy of nature. Thus, nearly total concurrence of symptoms of these crises seems to be especially remarkable.

Further, some of these symptoms were revealed in ecological crises of communities of terrestrial tetrapods at the end of the Permian (Sennikov 1991; Kalandadze & Rautian 1993b), and in a set of groups of marine invertebrates.

### List of Symptoms of Ecological Crises

1. Ecological crisis (preparatory phase, according to Rasnitsyn 1988, 1989) is preceded by:
  - 1.1 Increase in rate of formation of taxa (see symptoms 2.2.1, 2.2.2, 2.2.5, 3.2, and 4.2);
  - 1.2 Increase in extinction rate outstripping rate of formation of taxa. As a result, growth of number



- of accumulated taxa continues (see symptoms: 2.1, 3.1 and 4.1);
- 1.3 Occurrence of interzonal ecological lacunae at the borders of adaptive zones. A comparatively large number of them either remains open for an extended time or is used by the founders of the future active destroyers of the former structure of communities (see symptoms 2.2.4 and 2.2.5);
- 1.4 Decrease in stability (increase of vulnerability) of the *de novo* communities to the endogenous disturbances and exogenous effects (see symptom: 1.1-1.3, 1.6, 3.5, 4.4);
- 1.5 Relative continuity of biota of all the lands subjected to the crisis (uniformity of the main features). Global crisis is preceded by a biogeographical 'Pangea' (conjunction of all the continents);
- 1.6 Large ecological crisis is preceded by smaller crisis or crises (see symptom 4.4).
2. In the temporal vicinity of ecological crisis (preparatory, paradoxical, dramatic, and calming phases, according to Rasnitsyn 1988, 1989) the following specific peculiarities are observed.
  - 2.1 Extinction of a large number of previously widespread taxa including those of higher level (see symptoms 1.2, 3.1 and 4.1).
  - 2.2 The origin of:
    - 2.2.1 a large number of taxa, including those of high level (see symptoms 1.1, 3.2, and 4.2);
    - 2.2.2 a large number of short-living taxa not appearing in the paleontological chronicle for a long period, including those of a comparatively high level (mainly at the level of family, during large crisis) (see symptoms 1.1, 3.2 and 4.2);
    - 2.2.3 taxa regularly occurring in the paleontological chronicle only in temporal vicinity of crisis (see symptoms 3.4-3.8);
    - 2.2.4 crucial ecological novelties, in the case of large crisis causing considerable consequences to further history of the biosphere (see symptoms 1.3 and 2.2.5);
    - 2.2.5 the majority of future ecological dominants either before or after the crisis (see symptoms 1.1, 3.2 and 4.2);
  - 2.3 Increase of share of taxa surviving to the present, and a decrease of their geographic range (see symptoms 2.4 and 2.6);
  - 2.4 Vicariance of a set of ancient taxa of high taxonomic level by their phylogenetic successors of the same level (see symptom 2.6);
  - 2.5 Increase of share of phylogenetic relicts, connected with increasing archaic characters of biota, which is especially typical for the apogee of crisis (see symptoms 3.4-3.8);
  - 2.6 The change of ecological dominants manifested in transition of a set of taxa from category of rare and the rarest into the category of regularly occurring in the fossil record, and vice versa (see symptom 3.5);
  - 2.7 Abrupt change of the taxonomic composition of the biota and that of dominant communities during a comparatively short interval of geological time; the larger the crisis, the sharper the change, (see symptoms 1.1, 1.2, 2.1-2.6, 3.2, 3.3, 4.1, 4.2).
3. The apogee of ecological crisis (paradoxical phase, according to Rasnitsyn 1988, 1989) is characterized by:
  - 3.1 Decrease in the rate of extinction due to symptom 3.4 (see symptoms 1.2 and 4.1);
  - 3.2 Abrupt decrease in the rate of formation of new taxa, outstripping the decrease of rate of extinction and leading to reduction of the number of accumulated taxa (during large crisis not only of species and genera, but also families) (see symptoms 1.1, 2.2.5, and 4.2);
  - 3.3 Abrupt decrease in the biotic diversity connected not so much with the increase of extinction rate of taxa, but mainly with the decrease in the rate of their emergence (see symptom 3.2);
  - 3.4 Decrease in intensity of competition dependent on the density of population (see symptoms 2.2.3, 2.5 and 3.1);
  - 3.5 Decomposition of the pre-existing structure of communities, i.e. succession system, the structure of adaptive zones and ecological niches (see symptoms 1.4 and 4.4);
  - 3.6 Loss of phylogenetic and ecological specialization of a set of taxa; during a large crisis many lost; due to symptom 3.5;

- 3.7 Decrease in the ecological valency and increase in the probability of extinction of highly specialized cenophilic species, owing to symptoms 3.5 and 3.6 (especially on the following stage of phylogenesis, owing to symptom 4.3);
  - 3.8 Increase in the ecological valency and decrease of probability of extinction of broadly specialized eurybiontic forms from ecotones (especially on the following stage of phylogenesis, in the conditions of symptom 4.3), first of all cenophobic species, due to symptoms 3.5-3.7;
  - 3.9 Disappearance of a set of taxa, that persisted during the crisis without considerable changes, due to symptoms 3.5-3.7;
  - 3.10 Active advance of ecotones into the remaining sites of former communities, owing to symptoms 3.5-3.8;
  - 3.11 Variegated mosaic of sites, retaining the preceding biota and organization of communities, to a greater or lesser extent, and vast ecotones of an uncertain structure of biota including the ancestors of future ecological dominants of communities following the crisis (see symptoms 3.5 and 3.10);
  - 3.12 Geographically widely spread localities, accompanied by low diversity biotas and weak biogeographic connections of taxa due to rarity of their occurrence in different localities (see symptoms 3.3 and 3.11).
4. Ecological crisis ceases by (dramatic and calming phases, according to Rasnitsyn 1988, 1989).
    - 4.1 Increase of extinction rate, owing to symptom 4.3;
    - 4.2 Sharp increase in the rate of emergence of new taxa outstripping the rate of extinction. It results in the restoration of growth in the rate of accumulation of number of taxa (see symptoms 1.1 and 3.2);
    - 4.3 Increase of the intensity of competition depending on the density of population (see symptom 3.4);
    - 4.4 The origin of a new biota (the communities of new type), which, if preceded by a severe crisis, appears to be short-lived; and soon (in the geological time scale) plunges into another crisis but of smaller scope (see symptom 1.6).

## References

- Benton, M. 1985. 'Mass extinction among families of non-marine tetrapods'. *Nature*, vol. 306 no. 6031, pp. 811-814.
- Benton, M. 1987. 'Mass extinction among families of non-marine tetrapods'. *Mém. Soc. Geol.*, no. 150, pp. 21-32.
- Benton, M. 1988. 'Mass extinction in the fossil record of reptiles: paraphyly, patchiness and periodicity. Extinction and Survival in the Fossil Record'. *Syst. Assoc. Spec. vol.*, no. 34, pp. 269-294.
- Fedonkin, M. A. 1991. 'Biosphere: the fourth dimension', *Priroda*, no. 9, pp. 10-18.
- Kalandadze, N. N. & Rautian, A. S. 1983. 'The Place of Central Asia in the Zoogeographical History of the Mesozoic', in *Iskopaemye reptilii Mongolii, Trudy Sovn. Sov. Mong. Palaeont. Expedicii* [Fossil Reptiles of Mongolia, Proc. Commom. Sov. Mong. Palaeont. Expedition], Nauka, Moscow, vol. 24, pp. 6-44, (in Russian).
- Kalandadze, N. N. & Rautian, A. S. 1993a. 'The Jurassic ecological crisis of community of terrestrial tetrapods and heuristic model of conjugate evolution of community and its biota', in *Problemy doautropogennoi evolyutsii biosfery* [The problems of preanthropogenic evolution of the biosphere], Nauka, Moscow, pp. 73-91, (in Russian).
- Kalandadze, N. N. & Rautian, A. S. 1993b. 'Conjugated evolution of Amphibians and Reptiles in the end of the Paleozoic and beginnings of Mesozoic', in *Problemy evolyutsii biosfery* [Problem of the biosphere evolution], Nedra, Moscow, pp. 34-39.
- Meien, S. V. 1987, *Osnovy paleobotaniki* [Base of palaeobotany], Nedra, Moscow, 403 pp.
- Rasnitsyn, A. P. 1988. 'The problem of global crisis of terrestrial biocenoses in the middle of Cretaceous period' in *Cretaceous biocenotic crisis and evolution of insects* [Mezovoi biocenoticheskii krizis i evolyutsiya nasekomykh], Nauka, Moscow, pp. 191-207.
- Rasnitsyn, A. P. 1989. 'The dynamics of families of insects and the problem of the Cretaceous biocenotic crisis', in *The sedimentary covering of the Earth in the Space and Time: Stratigraphy: Palaeontology* [Osadochnaya obolochka Zemli v prostranstve i vremeni: Stratigrafiya: Paleontologiya], Nauka, Moscow, pp. 35-40.
- Rautian, A. S. 1993. 'About the nature of genotype and heredity', *Zh. obshch. Biol.*, vol. 54 no. 2, pp. 132-149.
- Rodendorf, B. B. & Zerkhin, V. V. 1974. 'Palaeontology and protection of nature', *Priroda*, no. 5, pp. 82-91.
- Sennikov, A. G. 1991, *Early Tectodons of East Europe*, Cand. Sci. (Biol.) Dissertation, Palaeontological Institute, Moscow, 270 pp.
- Vakhromeev, V. A. 1988. 'Jurassic and Cretaceous Floras and Climates of the Earth', *Trudy GIN AN SSSR (Proc. Geological Institute, AS, USSR)*, Nauka, Moscow, vol. 430, 214 pp.
- Zherikhin, V. V. 1978. 'The development and change of the Cretaceous and Cenozoic faunistic complexes (Tracheata and Chelicerata)', *Trudy PIN AN SSSR (Proc. Palaeontological Institute, AS, USSR)*, Nauka, Moscow, vol. 165, pp. 198.
- Zherikhin, V. V. 1979. 'The use of palaeontological data in ecological forecasting', *Ekologicheskoe prognozirovanie* (Ecological forecasting), Nauka, Moscow, pp. 113-132.
- Zherikhin, V. V. 1987. 'Biocenotic regulation of evolution', *Paleontologicheskii Zh. (Moscow)*, no. 1, pp. 3-12.





## 2.2 Development of the Late Permian Marine Benthos in a Precrisis Situation

G. A. Afanasjeva and I. P. Morozova

### Abstract

Consideration in the changes of taxonomic diversity of articulate brachiopods, bryozoans, rugose and tabulate corals in the Late Permian permits recognition of symptoms of ecological crisis of the late Permian benthos and application of the Kalandadze/Rautian model in the analysis of the Permian–Triassic extinctions.

The reduction of biodiversity in the Late Permian was prolonged and gradual. We shall try to trace it as an example, for some groups of invertebrates, in order to compare real changes of marine fauna at that time with the taxonomic transformations of biota being the symptoms of an ecological crisis discussed by Kalandadze and Rautian.

Significant reduction of generic and family diversity of marine invertebrates began in the Midian (according to the Tethyan scale), especially in the latter part, i.e. approximately at the beginning or at the first part of the Kazanian of the International Time Scale. Definition of the Midian stage was based on fusulinids, ammonoids and conodonts. This paper examines the changes of marine faunal diversity during the Midian, Dzhulfian and Dorashamian of the Late Permian (fig. 1). We will look at the data on generic numbers of articulate brachiopods, bryozoans, rugose and tabulate corals. We chose these invertebrates partly because they were the most numerous and the most widespread groups of Paleozoic marine benthos, extinct entirely or nearly at the end of the Permian, and partly because we have available reliable data on their chronological distribution.

At the beginning of the Late Permian, in Kubergandian and Murgabian time, there was no appreciable reduction of either the total number or the number of *de novo* genera of articulate brachiopods, bryozoans, rugose and tabulate corals. Familial composition of these groups had not changed for some time. At each subdivision of the Early Permian, articulate brachiopods were represented by 96 to 113 genera, and 27–40 genera appeared for the first time. For bryozoans 70 genera and 15 *de novo* species, for rugose corals 80 and 16, for tabulates 30 and 6.

At the beginning of the Late Permian nearly the same level of diversity was retained, although the number of *de*

*novo* genera was slightly lower. In Kubergandian time 110 genera of articulate brachiopods existed, 28 of which appeared for the first time, for bryozoans correspondingly 67 and 6 genera, for rugose corals 64 and 12 genera, for tabulates 24 and 2 genera. In Murgabian times amongst the total number of articulate brachiopod genera were 116, 22 were first appearances, for bryozoans 70, 21, for rugose corals 70, 15, for tabulate 20, 6.

Reduction in the diversity of these groups, as mentioned above, began from Midian time. Although the total number of the genera was still rather high (brachiopods 98, bryozoans 50, rugose corals 68, tabulates 22), the number of *de novo* genera was reduced in many cases in bryozoans (7), rugose corals (2), tabulates (3), yet relatively significantly in brachiopods (27). The beginning of the extinction at the family level was characteristic for this time. The most significant extinction of families was observed in bryozoans. Among 26 families present in the Early Midian, only 9 survived into the Dzhulfian. For rugose and tabulate corals respectively 6 and 2; for brachiopods of 66 families, 20 became extinct.

During Dzhulfian and Dorashamian times the number of genera in all groups was sharply reduced. In brachiopods the total number of genera at these times was 60 and 23. In Dzhulfian times 5 genera, and in Dorashamian times 4 genera, appeared. For bryozoans in the Dzhulfian time 16 genera existed, and in Dorashamian 11; for rugose corals correspondingly 12 and 6 genera; for tabulates 6 and 5 genera. No new genera of bryozoans, rugose corals and tabulates appeared during these stages.

At the end of Dorashamian, all earlier genera of articulate brachiopods, rugose corals and tabulates disappeared. Only 4 genera of bryozoans crossed the Permian–Triassic

**Figure 1** Dynamics of generic number of articulate brachiopods, bryozoans, rugose and tabulate corals in the Late Permian

Stages Fossil groups	Kubergandian	Murgabian	Midian	Dzhulfian	Dorashamian
Brachiopods	110-28-22	116-22-45	98-24-43	60-5-41	23-4-23
Bryozoans	67-6-18	70-21-27	50-7-34	16-0-4	11-0-11
Rugoses	64-12-9	70-15-4	68-2-56	12-0-6	6-0-6
Tabulates	24-2-10	20-6-1	22-3-16	6-0-1	5-0-5

In every column the first cipher means the total number of genera, the second the number of first appeared genera, the third the number of extinct genera.

boundary. Extinction took place also at the ordinal level. Among articulate brachiopods the orders Orthida, Strophomenida, Chonetida, Productida, Spiriferida, either became extinct or were severely affected. Bryozoan orders Rhabdomesida, Cryptostomida, Fenestrada and all rugose corals and tabulates became extinct at the end of the Permian.

Cited data, in our opinion, can indicate a recognition of the first (1.6), the second (2.1) and the third (3.3 and 3.9) symptoms of ecological crisis after Kalandadze and Rautian in this volume.

According to symptom 1.6, a large ecological crisis was forestalled by the crisis of a smaller scale. It is possible, apparently, to estimate a smaller crisis compared with that of the Permo-Triassic, the situation in Midian time when the extinction of marine invertebrate families took place.

Symptom 2.1 is connected with an extinction of numerous, formerly widespread, taxa including those of higher taxonomic levels. This symptom is recognized most easily because the extinction was of orders, whose representatives were widespread and even dominant during the late Paleozoic.

Symptom 3.3 is characterized by a sharp reduction in taxonomic diversity of the biota at the height of the crisis, which was connected rather with the lowering of the origination rate of the taxa than with their extinction rate. In fact, at the Permian-Triassic transition the number of new genera of articulate brachiopods was sharply reduced. So, in Midian times 27 genera appeared for the first time, at Dzhulfian only 5, and at Dorashamian 4. At the same time the extinction rate was gradually decreased: at Midian 43 genera became extinct, at Dzhulfian 41 and at Dorashamian 23. As to Bryozoa, Rugosa and Tabulata at the Dzhulfian and Dorashamian new genera did not appear on the whole. The extinction rate of these groups sharply increased in Midian times and then sharply lowered at the Dzhulfian and Dorashamian. In the Murgabian 27 genera of Bryozoa, 4 genera of Rugosa and 1 genus of Tabulata became extinct; in the Midian 34 genera of Bryozoa, 56 genera of Rugosa and 16 genera of Tabulata; at the Dzhulfian 4 genera of Bryozoa, 6 genera of Rugosa and 1 genus of Tabulata; at the Dorashamian 11 genera of Bryozoa, 6 genera of Rugosa and 5 genera of Tabulata.

Symptom 3.9 is extinction of a number of taxa which, in fact, had been preserved without essential changes. For all those taxa under review that did not become extinct, their biomass and geographic extent was so reduced that they appeared out of the taphonomically reliable part of the paleontological chronicle (i.e. they became rare). Apparently bryozoans in the order Tubuliporida belonged to such taxa. Some specialists suggested that this group of Bryozoa had become extinct at the end of the Paleozoic. Nevertheless, some genera very similar to tubuliporids, undoubtedly their descendants, have been described from

the Triassic. Until recently it was considered that bryozoans in the order Cystoporida became extinct at the end of the Permian. However, a find in the Upper Triassic of a new genus in the Palaeozoic family Fistuliporidae (Schafer & Fois 1987) indicates that cystoporids also survived the Permo-Triassic crisis. It is generally accepted that *Tetracorallia* became extinct at the Permo-Triassic boundary. However, the latest representatives of tetracorals polyphyllins — had some characters of septal structure similar to the Middle Triassic Scleractinia, because of which *Tetracorallia* has been considered an ancestral group for Scleractinia.

Brachiopod genera in the orders Rhynchonellida, Athyridida and Terebratulida, which were the connecting links between the Late Permian and Early Triassic taxa are absent in the paleontological record. Judging by the paleontological finds, no one brachiopod genus crossed the Permo-Triassic boundary. Obviously all those listed examples of disappearance from the paleontological record in the Late Permian of the ancestors of Triassic forms occurred due to pseudo extinctions — these forms became extinct by giving rise to other taxa.

Consideration of the real changes of taxonomic diversity in some groups of marine benthos at the time before the crisis situation of the Late Permian allowed us to recognize several symptoms of ecological crises described by Kalandadze and Rautian. Some of the other symptoms are impossible to recognize in our material, but we have no data which will contradict them. Some of these symptoms have a relation only to the post-crisis situation. Nevertheless, the coincidence even of some symptoms apparently can give support to an application of the proposed model as a whole to the analysis of the Late Permian extinction.

## References

- Schafer P. & Fois E. 1987, 'Systematics and evolution of Triassic Bryozoa', *Geologica et Palaeontologica*, no. 21, pp. 173–225.

# **Ecosystem Reorganization and Biome Formation**

**3**







### 3.1 Phylogenesis and Phylocenogenesis

V. V. Zherikhin

#### Editor's note

*This paper has not been changed over how it was initially submitted in order to allow the author's full philosophical ideas to be presented in his original form.*

In spite of increasing interest in natural community changes, the current state of theory of community evolution (the phylocenogenesis after Sukachev 1942) still remains unsatisfactory. It is impossible to discuss this problem in detail in a brief paper; here I try to show that its present state is mainly a result of conceptual puzzling about the theoretical backgrounds in evolutionary synecology and propose some attempts for its possible solution.

#### What is evolution?

A confusion begins with the basic concept of evolution. In natural sciences other than biology, evolution is treated in accordance with etymology as the deterministic process of irreversible changing in a system which may be predicted with a knowledge of its initial state and environmental influences. The evolutionary concepts in astrophysics, planctology, geology, etc. can be referred to as illustrations.

The biological view on evolution is different as is evident from the fact that the ontogenesis, which relates to the above idea, is not considered to be an evolutionary process. Modern biology treats the evolution as a spontaneous emergence of *a priori* unpredictable ontogenetic program changes, which are constantly reproducible and irreversible in successive generations. In these terms, the inanimate things do not evolve: they have ontogeny but lack phylogeny. Indeed, similar stars or rocks are not monophyletic: they have similar ancestors but no common ancestor. The exception is provided by the results of biological activities, which are derived as biological evolution by-products and are as unpredictable. They should be considered in this respect together with the living world even if they were as inorganic as free oxygen; and if the photosynthesis is monophyletic (which is possible if symbiogenetic chloroplasts were originally monophyletic), so the production of atmospheric oxygen should be monophyletic, too, although oxygen molecules are certainly polyphyletic in any case.

Still another meaning of evolution exists in descriptive biology when one describes, for example, the evolution of the skull or digestion. Here an evolving entity lacks its own ontogenetic program and can not reproduce itself outside the whole organism, which controls its possible changes. Though a selective value of individual structures is still discussed in many papers, this is rather a

matter of homage to the tradition. The modern evolutionary paradigm supposes no selection for a beak longer or legs shorter: the only thing more important for the natural selection is a relative reproductive success resulting from a multitude of different and partly controversial effects of particular features which, however, are not the subjects of selection *per se*.

The multispecific biological assemblages are, undoubtedly, variable in time in different ways, including some irreversible transformations. The question is which, if any, kind(s) of these changes may be regarded as evolutionary ones in the biological sense of the term.

#### What is the community?

Because of the very complex nature of synecological systems, their structure and changes can not be described by a single universal model, and a set of complementary models is necessary to analyse the phenomena of different natures separately. Surely, one can demonstrate that this concept of community makes the biological evolutionary paradigm inapplicable; and it is the commonest logic to doubt or reject the existence of community-level evolution. However, it does not mean that the same would be true for any other concept, so the problem should be discussed in a more general way. To do so, it is necessary to look at different models from a point of view of their validity for evolutionary challenges.

There are two major alternative types of synecological models. The biogeocenotic models incorporate both biotic and abiotic components of an ecosystem as the equivalent ones, while the biocenotic models are restricted to living and dead organisms (plus their metabolites which exclusion makes the model incomplete). Undoubtedly, the biocenose is an ideal construction, which actualises only in the form of certain biogeocenoses; but such ideal schemes (the ideal gas, for instance) are necessary to analyse any complex system or process. In particular, in the biogeocenotic models, biological evolution of their biotic constituents and deterministic evolution of abiotic ones have to add up to give a complex, resultant pattern which can not be interpreted uniquely in the terms of evolutionary biology. Thus, the evolution of biogeocenoses as the landscape units is certainly not biological evolution, and only biocenotic models picking out the biotic component of the process alone may be of interest for our challenge.

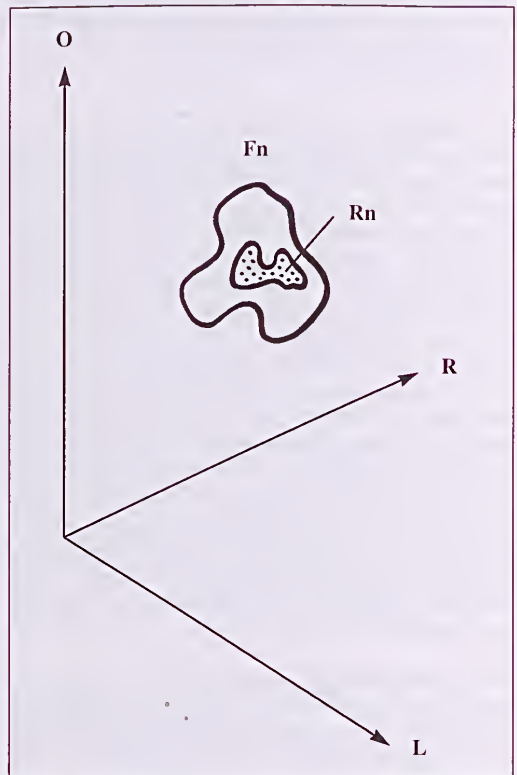
The communities can be also represented with either morphological (geobiological) or functional terms. At once, the former way seems to be 'more biological'; however, many morphological features of a community, such as its spatial configuration, area, and borders are

under strong environmental control. A biocenose is pouring into an environmental mould available now and here, and if the geobiological approach is following consistently, it leads necessarily to a biogeocenotic-type model. This is one of the most important (but not the single) source of the common scepticism about the community evolution among the geobotanists. On the other hand, a functional view dealing first of all with matter and energy flows is equally applied to both biocenotic and biogeocenotic models in spite of its connection (mostly historical) with the ecosystem concept. It could be pointed out that strictly energetic models are oversimplified and unrealistic because of the ignoring of low biomass population, which may be functionally important as ecosystem regulators (parasites, for instance), and the entire diversity of biotic interactions would be taken into account to make a model more sophisticated.

The question of elementary structural units being used in models is next. Communities are routinely regarded as assemblages of species or their local populations. One problem is that neither the species nor the population concept is an ecological one. The notion of species is either taxonomic or evolutionary, whilst populations are defined usually as reproductive units. Their ecological inadequacy is evident just from the fact that universality of both concepts is often doubted for asexual organisms, where an ecological elementary unit would be independent from the mode of reproduction. Another factor is even more important: the species (as well as populations) is essentially individualistic in their ecological distribution, so that in the general case their ecological tolerance limits do not coincide either one with another or with the limits of certain communities. Thus, the continualistic community concept, which is so widely accepted now, seems to be an unavoidable corollary of applying this language to community description. It often leads to the conclusion that community evolution would hardly be regarded as something more than a simple sum of largely independent evolutionary histories of the constituting populations. However, an individualistic species or population pattern does not mean necessarily that the communities can not be represented as more discrete units in an alternative way. The multidimensional niche concept generally accepted in ecology after Hutchinson (1965) resolves this problem quite easily: the ecological equivalent to the species is its fundamental niche, whilst a realised niche corresponds to the local population. So, a community would be represented as a concert of realised niches instead of an assemblage of populations. Though there may be some identical niches (and even when their owners are not conspecific) in different communities, the entire niche space structure in each case is formed by the community so that the problem of incongruence in limits is eliminated at once. The failure of species and population-based models in evolutionary synecology shows that ecology uses its own language to avoid conceptual puzzlings.

The misuse of taxonomical language is also the source of another kind of inaccuracy. The taxocenes as sets of taxonomically related members of the same community (and themselves often wrongly called the communities) are pragmatic descriptive units lacking any real ecological content. It is just evident for, say, fish or insect 'communities', and even the phytocenes (plant 'communities') to coincide with the natural ecological group of primary producers only in part because of the existence of both non-autotrophic plants and autotrophic non-plants (prokaryotes). Clearly, the taxocenes do not evolve as units (and by the way, it is another source of geobotanists' criticism for the community evolution concepts).

Because the niche is treated somewhat differently by different authors, some comments are necessary. Principally, a niche may be given by an endless enumeration like the following: the sedentary benthic filtrating suspension-feeder, with necessary diet including a, b... (optimal c, d...), passively protected with the strong carbonate shell, inhabiting rocky substrates under the depth limits e to f (optimal g to h), temperature i to j (optimal k to l), salinity m to n (optimal o to p). The theoretically infinite dimension number is impractical and produces some problems even when used in models. However, in a generalised model those dimensions to a



**Figure 1** The generalised concept of the fundamental (Fn) and realised (Rn) niche: O - organisation of the niche owners, R - resource, L - non-resource limiting factors (Zherikhin 1994).



first approximation may be reduced to the three basic ones (Zherikhin 1994), namely the resources (e.g. food, oxygen, preferable substrates), the non-resource limiting factors (e.g. temperature, acidity, predation), and the organisation of the niche owner (e.g. feeding mechanisms, locomotion, digestion, behaviour). In doing this, the fundamental niche is expressible by the basic variables values at the global, and the realised niches - at the local scales (fig. 1). It would be noted that this niche meaning excludes the 'vacant niche' concept, which is, inconsistent with the Hutchinson's niche definition; the potential niche space would be described in terms of licences as proposed by Levchenko and Starobogatov (1990).

Within a community the more closely interrelated niches form a complex pattern of the functional blocs such as the guilds, consorts, trophic webs and levels, regulatory blocs, microsuccessions, etc. Those blocs are partly hierarchically subordinated and partly mutually intersected in the ecological space, with each niche being incorporated concurrently into a number of different blocs. The total number of niches and interactions in natural communities is usually too large to be reflected exhaustively by a model, but principally the structure of any bloc and its interactions with others may be presented with any reasonable degree of accuracy.

The communities can not reproduce themselves outside certain successional series. Most communities are intrinsically unstable on an ecological time-scale because of depleting of some resources and overproducing of others by the community members. If the ecological successions are taken in the strict sense as the autogenic ones (with any exogenous 'successions' being treated as the disturbances), this imbalance in biogeochemical cycles has to be their prime mover (Vakhrushev & Rautian 1993). A climax community normally keeps its turnover near an equilibrium state indefinitely, but after being disturbed, it also can be restored through certain ecological successions only. Thus, the successional systems, which are the regional ensembles of successional related communities (Razumovsky 1981) should be regarded as the minimal self-reproducing biocenotic units. Besides 'vertical' successions, the communities within a system are interconnected also 'horizontally' by the organisms exploiting more than one community concurrently. The most common models restricted to vegetation alone are purely descriptive and

ignore the very mechanism of successions. Any causal model of successions has to cover all trophic levels of all successional related communities because the successions are originated from their combined activities. Because the biological evolution concept is appropriate to the self-reproducing systems only, it is wittingly irrelevant to an individual community or other units below the successional system level.

One more important point concerns the problem of integrity. The interrelations between niches are either of an opportunistic or of a specialised (co-adapted) type, including indirect diffuse coadaptations to the latter. Principally, the multispecific assemblages would constitute a continuum from the totally accidental and opportunistic up to totally co-adapted ones; the former may be called the ideal groupings and the latter, biocenoses. The more co-adapted the community is, the more integral it is. Any actual community occupies a certain intermediate position between both theoretical extremes and manifests concurrently both continualistic and holistic properties. So, its estimation as a community or a grouping is relativistic as may be seen by the example of anthropogenic assemblages. The aboriginal 'weedy' assemblages in the Old World would be regarded as groupings in comparison to the natural native communities; however, in regions with less ancient agriculture as in North America or Australia, they demonstrate more integrity in comparison to the native weedy groupings which are younger and less co-adapted.

The successional systems may be arranged in the same manner, from chaotic accidental successions of ideal groupings up to entirely deterministic and regular successions of mutually co-adapted ideal biocenoses (fig. 2). An ideal successional system should be crowned with an ideal climax, which is absolutely intrinsically stable due to its precisely balanced turnover. Systems with more than one climax stage are possible too. A succession may be ceased or reversed accidentally by an outer force before reaching the climax. Any non-climax stage may be stabilised externally for an indefinite period as a subclimax maintained by continuous removing of its surplus production with washing out, burning, or other extrinsic actions. The distinction between the climax as the intrinsically stable final stage and the subclimax as the extrinsically stabilised one is worthwhile only in biocenology and loses its meaning at the biogeocenotic scale where water flow and wind are considered within

Assemblage types	ideal groupings	actual groupings	cyclic systems	systems with subclimaxes	systems with climaxes	ideal communities
Successions	chaotic	irregular	cyclic	linear	linear	linear, strictly deterministic
Stable final stages	no	no	no	extrinsically stabilized	intrinsically stabilized	intrinsically stabilized

Figure 2. The continuum of integrity of multispecific assemblages.

the same system together with the predators and decomposers. In a less co-adapted system there is no climax, and subclimaxes are the only stable stages possible; if any continuous external stabilisation is absent, such successions are cyclic. Different kinds of final stages may coexist within the same system forming transitions between the major types mentioned above.

### What is the community-level evolution?

Thus, if the biological evolution concept may be applied at the community level at all, it would be tested for a functional biocenotic model of successional systems based on realised niches as the elements; any other attempt would be logically incorrect.

The successions are complex and variable, but they are not chaotic. Their predictability decreases in general with an increase in continuity of successional communities (fig. 2); nevertheless, even the successions of actual groupings, in fact, always exhibit some regular trends. The parallel between successions and ontogenesis noticed firstly by Clements as early as in 1916 has been underestimated by more recent authors. Both processes are similar, indeed, in their being deterministic, stereotypically reproducible and equifinal, with most deviations self-controlled and self-corrected by the system, so that various paths lead to essentially the same final stage. However, a peculiar feature of the successions in comparison to ontogenesis is that all stages occur simultaneously within the same individual system; so a succession may be described as an ontogenesis in parts, proceeding as continuous asynchronous regenerations, somewhat like vegetative rhizome reproduction in plants.

In fact, regeneration is a special case of self-reproduction in some cases hardly separable from budding and other kinds of asexual reproduction. The commonly accepted view rejecting any community-level mechanisms analogous to the genetic program of organisms would be valid for the individual communities, but not for the successional systems, because any self-reproduction supposes the existence of such a mechanism with necessity. The question of its nature is crucial for evolutionary biocenology if we take the evolution as the changes in an ontogenetic program.

I suggest that biocenotic 'genome' is difficult to recognise not because it is too small and local, as in most organisms where it has not been detected until this century, but on the contrary, because it is too large and unlocalised from the point of view of a human observer. Like the virus particles, the successional systems are entirely built from their genetic material: the very ensemble of niches constituting the system structure also maintains its constancy in the course of continuous regenerations. This higher-order genotype is based on the entire gene pool of co-existing populations of different species; but it operates in a non-additive way due to complex niche interactions. It is not a simple sum of populations or their

niches but an integral composite system like an organism genome, which also is not a simple sum of a few species of atoms but a complex integral chemical system. As long as the ensemble of realised niches remains the same at a regional scale, the functional structure of all communities existing here as well as their successional order would constantly reproduce themselves because the constant niches should combine one with another by the constant way. Consequently, any irreversible and reproducible change in the niche set has to be considered as a microevolutionary event at the community level.

There are five possible basic types of phylogenetic events which correspond rather well to the 'ways of phylogenesis' after Bykov (1978). Those basic types are as follows:

1. Esogenesis, i.e. a realised niche shift by a conversion of its interrelations to other niches (Bykov restricts it to the limits of the community but here it is treated more broadly, including the entire successional system);
2. Specio genesis, i.e. a realised niche transformation caused by changes of the corresponding fundamental niche;
3. Elision, i.e. a realised niche loss;
4. Invasion of a realised niche (regarded by Bykov together with the elision under the common name of transgenesis);
5. Substitution of one realised niche to another through competitive species replacement (not considered as a peculiar case by Bykov).

Any primary event may provoke a number of secondary effects both in the directly related niches and (by diffuse effects) within the entire niche ensemble. The final effect on the system may range from a negligible up to a very destructive one. It would be stressed that the changes along any basic niche axis are equally important phylogenetically.

Those basic events are the simplest microevolutionary acts like the mutations. The successional systems rejuvenate but not multiply themselves so that these acts operate in the system lifetime like the somatic mutations in an organism. A similar way of evolution occurs in clonal organisms where the entire clone may be considered as a genetically uniform 'evolutionary individual'; the mutations disrupt its uniformity, providing a base for competition between different genotypes. So, a peculiar type of natural selection would act inside the evolving system. A competition between successional systems would also occur in space and time resulting in an expansion of more successful systems at the sacrifice of less successful ones. However, in the absence of propagation it should be the original



Darwinian selection as the survival of the fittest rather than the differential reproduction of the modern synthetic evolutionary theory.

The specio genesis, elisions, and esogenesis are easily comparable with the common genetic changes of organisms where the genes also may be changed spontaneously, or lost, or their effects may be modified by interactions with other genes. As regards the invasions and substitutions, they seem to be more or less analogous to genetic transductions when an alien gene (or genes) is included in the genome system. The role of transductions in evolution of higher organisms is disputable but they are certainly common among the prokaryotes. So, the basis events seem to be not dissimilar principally between the organism and community levels.

The combining elementary events give a resultant macroevolutionary pattern. The macrophylocenogenetic phenomena may be roughly classified into three main types regarding their effects on the evolving system integrity:

1. Phylocenogenetic constructions, when the integrity is increasing and the entire system is evolving within a grouping-community continuum towards the co-adapted community pole;
2. Phylocenogenetic destructions, when the integrity is decreasing and the system is evolving to the opposite, grouping pole of the continuum (fig. 2);
3. Phylocenogenetic transformations, when the integrity is not changing sufficiently and the position of the system within the continuum changes slightly or fluctuates without a definite trend.

A simple qualitative model of the phylocenogenetic constructions has been developed recently (described briefly by Zherikhin 1992; a more detailed version is in press), and a general qualitative model of destructions is in progress now. Both models can not be described in detail here, and some important points only should be stressed.

The construction model based mainly on changing selection patterns favouring different ecological strategies predicts a strong tendency to mutual adaptation of realised niches inside an accidental grouping but only under the predictable abiotic environments. This trend would occur even under a minimal initial heterogeneity of the assemblage in regards to exploitation of different habitats available, and a progressive specialisation to habitats accompanying a divergence of niches and their owners is expected. The habitat diversity would increase due to a biogenous creation of new ones.

During this community self-organisation process any group of more co-adapted niches may play the role of a 'crystallisation centre' because of its being the most

predictable environment nucleus for other niche owners; however, a conflict between the structures forming around different primary centres is possible.

At a larger scale, more co-adapted communities would extend their influences over neighbouring, less co-adapted ones. Therefore, groupings in general will tend to disappear due to their progressive absorption by communities. An interesting model of such a process has been developed recently by Kalandadze and Rautian (1993), who illustrated it with some paleontological data on vertebrates. However, a conflict between alternative niche systems would stop this absorption process before groupings would be completely incorporated into communities. The communities would become less stable and less predictable near their borders, and at a contact zone (ecotone) between two or more different biocenoses neither of them are constantly stable. Consequently, the ecotones between communities and especially between different successional systems are permanently occupied by more accidental assemblages with less predictable niche structure and interactions. Because the natural ecotones are usually rather restricted in space, their area may be often too small to support populations of large-sized organisms. So, it is expected that vertebrates or large trees would follow the Kalandadze-Rautian model, whereas herbs or invertebrates would not.

Regarding the destructions, a stepwise course of the process with consecutive autonomisation of progressively diminishing and loosely interacting one with another blocs of co-adapted niches is predicted. Some free relict blocs inherited from other system(s), which may have been destroyed, persist for an indefinite period on the background of groupings being the potential 'crystallisation centres' there.

The transformation is a complex process resulting from the combining destruction and construction on a relatively limited scale. An important special case, which may be called the succession pruning, is discussed in more detail in another of my papers in this issue.

### Phylogenesis and phylocenogenesis: the interrelations

When phylocenogenesis is regarded as changes in realised niches, the phylogenesis would be defined in the same terms as changes in fundamental niches along the organisation axis. All realised niches of the same species must be located within the volume of its fundamental niche. Hence, it follows that phylogenetic and phylocenogenetic events are related but not uniquely related. By definition, the esogenesis is a phylocenogenetic event not accompanied by any phylogenesis of the fundamental niche owner; its possibilities are strictly limited by the fundamental niche configuration. The specio genesis, on the contrary, is directly based on phylogenetic transformations. However, a phylogenetic event can not affect those successional systems where the realised niche of the species remains



unchanged: for example, the decrease of the fundamental upper limit of the temperature tolerance from 35° to 30°C is of no immediate importance for a system where the actual temperature never exceeds 20°C although it may influence its response to future climatic changes. The elisions, invasions, and substitutions may be phylogenetically caused or not, and in both cases are unrecognisable within a successional system. For instance, an invasion effect depends on niche characteristics of the invader but not on its being a newly originated species (the phylogenetic event) or a newly penetrated immigrant (no phylogenetic events).

Thus, there may be:

1. A non-phylogenetic phylogenogenesis;
2. A non-phylogenetic (in certain successional systems only) phylogenesis;
3. A phylogenogenesis directly resulted from phylogenesis.

However, the phylogenogenesis is never independent from the past phylogenetic history of the niche owners. The organisation, which is one of the basic niche dimensions, reflects the past ecological experience in the phylogenetic line for a very long time, and it seems to be a very important factor of preadaptations. Many adaptive challenges affecting evolution of a species are, in fact, not new ones for it in the phylogenetic time. The rapid acquirement of pesticide resistance provides a possible illustration. This phenomenon is known now in many herbivorous and detritivorous taxa but seems to be relatively rare among carnivores. The acquiring of various natural substances, protective against herbivores, is a common evolutionary strategy in plants; thus, adaptations to different toxic chemicals occur continuously in evolutionary history of herbivores and detritivores (Rhodes & Gates 1976). Probably this is because they are much more successful in their adaptations to man-made chemicals in comparison to predators of different directions of their niche transformations; it may be predicted that the probability of co-adaptations between species would be roughly proportional to their common past experience.

On the other hand, the biocenotic environments restrict sufficiently the possibilities of phylogenetic changes in populations constituting the community. There are at least four hypothetical community-level mechanisms which would limit the phylogenesis rates and directions (Zherikhin 1987). Firstly, an increasing environmental predictability inside a community strengthens the stabilising component of the natural selection favouring more conservative genotypes and maintaining the equilibrium between different gene frequencies within a population.

The mutual stability reinforcement has to occur between the population and community levels, because the more genetically stable the constituting populations become the more stable and predictable the interior community environments become leading to further increasing in the stabilising selection, and so on. Secondly, a community may suppress the genetic drift by an effective population density regulation. Thirdly, the probability of any drastic phylogenetic novelties is minimised by dense niche packing, which channelizes the changes mostly to a progressive specialisation. Finally, the probability of evolutionary 'chain reactions' (i.e. consecutive phylogenetic transformations in numerous populations of different species initiated by single phylogenetic change) is low because the parallel functional paths duplicating each other in a community makes it rather resistant to a single specio-genetic event. A comparison of experimental and paleontological data on insect evolution shows that its average rate in the late Cenozoic was roughly five to six orders of magnitude lower than the potentially possible ones (Zherikhin 1987). This was probably a result of the community-level regulation of phylogenesis although the relative contribution of different mechanisms is not clear.

All those hypothetical regulating mechanisms have two important features in common: they are stochastic, and their efficiency would increase with the increasing integrity of the entire biocenose. The stochasticity supposes that the reliability of regulation is, with other things being equal, a question of time: the longer is the time of the system existence, the more is the probability of accidental uncontrolled phylogenetic events potentially destructive for the system. If so, the spontaneous phylogenetic destructions caused by phylogenetic processes inside successional systems should be unavoidable some time or other even when there are no changes in the extra-systemous environments. The relative role of spontaneous and exogenous destructions is not known definitely though the former seem to be rare. A spontaneous nature of a large-scale destruction of non-marine communities in the mid-Cretaceous has been hypothesised (Zherikhin 1978, 1993).

The dependence of the community-level phylogenetic regulators on the integrity of the biocenose supposes that the less co-adapted is the assemblage the more rapid and drastic phylogenetic transformations would occur inside it. In other words, the phylogenetic constructions would progressively suppress phylogenetic changes in the constituting populations while the phylogenetic destructions would provoke more substantial and numerous phylogenetic events. So, an ecological crisis regardless of its primary cause would initiate a consecutive phylogenetic crisis at a roughly proportional scale (Zherikhin 1978, 1993).

## References

- Bykov, B. A. 1978, *Geobotanika, (Geobotany)*, Nauka Press, Alma-Ata (in Russian).
- Clements, F. E. 1916, 'Plant succession: an analysis of the development of vegetation', *Carnegie Inst. Washington Publ.* 242, pp. 1–512.
- Hutchinson, Y. E. 1965, *The niche: an abstractly inhibited hypervolume. The Ecological Theatre and the Evolutionary Play*, Yale Univ. Press, New Haven, pp. 26–78.
- Kalandadze, N. N. & A. S. Rautian 1993, 'The Jurassic ecological crisis of the terrestrial vertebrate community and a heuristic model of the attended community and biota evolution', *Problemy doantropogennoi evolutsii biosfery (The Problems of Pre-anthropogenous Biosphere Evolution)*, ed. A. Y. Rozanov, Nauka Press, Moscow, pp. 60–95 (in Russian).
- Levchenko, V. F. & Ya. I. 'Starobogatov 1990, Succession changes and evolution of ecosystems (Some problems in evolutionary ecology)', *Zhurn. Obshchei Biol.*, vol. 51 no. 5, pp. 619–631 (in Russian).
- Razumovsky, S. M. 1981, *Zakonomernosti dinamiki biotsenozov (The Pattern of Biocenose Dynamics)*, Nauka Press, Moscow (in Russian).
- Rhodes, D. F. & R. G. Gates 1976, 'A general theory of plant antiherbivore chemistry', *Rec. Adv. Phytochem.*, vol. 10, pp. 168–213.
- Sukachev, V. N. 1942, 'The development concepts in phytocenology', *Sovetskaya Botanika*, no. 1, pp. 3–12 (in Russian).
- Vakhrushev, A. A. & A. S. Rautian 1993, 'A historical approach to the community ecology', *Zhurn. Obshchei Biol.*, vol. 54 no. 5, pp. 532–555 (in Russian).
- Zherikhin, V. V. 1978, 'Development and changes of Cretaceous and Caenozoic faunistic assemblages (Tracheata and Chelicerata)', *Trudy Paleontol. Inst. AN SSSR*, no. 165, pp. 1–198 (in Russian).
- Zherikhin, V. V. 1987, 'Biocenotic regulation of evolution', *Paleontol. Zhurn.*, no. 1, pp. 3–12 (in Russian).
- Zherikhin, V. V. 1992, 'Historical changes in insect diversity', in *Biologicheskoe raznoobrazie: podkhody k izucheniyu i sokhraneniyu (Biological Diversity: Approaches to Investigation and Conservation)*, *Materialy Konferentsii Botan. Inst. RAN i Zool. Inst. RAN 14–15 maya 1990*, ed. B. A. Yurtsev, St Petersburg, ZIN RAN, pp. 53–65 (in Russian).
- Zherikhin, V. V. 1993, 'Possible evolutionary effects of ecological crisis: paleontological and contemporary data', in *Aerial Pollution in Kola Peninsula. Proc. Internat. Workshop. Apr. 14–16, 1992, St Petersburg. Kola Sci. Centre, Apatity*, eds M. V. Kozlov, E. Haukioja, V. T. Yarmishko, pp. 53–60.
- Zherikhin, V. V. 1994, 'Evolutionary biocenology: the problem of model choice', in *Ekosistemnye perestroiki i evolutsiya biosfery (Ecosystem Restructures and the Evolution of Biosphere)*, 1, eds A. Y. Rozanov, M. A. Semikhatov, Nedra Press, Moscow, pp. 13–20 (in Russian).





### 3.2 Succession Pruning: a Possible Mechanism of Biome Diversification

V. V. Zherikhin

#### *Editor's note*

*This paper has not been changed over how it was initially submitted in order to allow the author's full philosophical ideas to be presented in his original form.*

Communities coexisting at the regional scale are organised into a successional system (Razumovsky 1981), which is the minimal self-reproducing biocenotic unity (Zherikhin, this issue). At any instant, the complete set of successional stages occurs within the successional system area. Their spatial pattern is peculiar for a landscape. A limited number of stages dominating within the landscape may be called the landscape-forming ones. Because the spatial distribution of different communities is determined by physiography the landscape-forming stages are not necessarily the true, intrinsically stable climaxes (Zherikhin, this issue) but may well be subclimaxes or even form a cyclic succession. In other words, the landscape-forming communities are biogeocenotically, but not necessarily biocenotically, stable. The landscape distribution of climaxes depends mainly on the ratio between the disturbance frequency and the succession rate, being negatively correlated with the former and positively with the latter. Similar disturbance patterns give rise to a similar share of different successional communities even in geographically remote areas occupied by different successional systems. According to the major successional seres the xeroseral, mesoseral and hydrosesal landscapes may be recognised, with additional divisions based on the dominance of early, mid or late successional stages of the sere.

Biomes are usually treated as physionomically similar community types dominating large territories. A number of biomes are commonly recognised, like the tropical rain forest, tropical deciduous forest, temperate broad-leaved forest, coniferous forest, savanna, steppe, desert, tundra and polar desert biome. However, superficial similarity is not a good criterion, and some disagreement on biome classification is not surprising. The functional (ecosystemous) approach to the distinction of biomes based on matter and energy turnover would be much more heuristic, although, unfortunately, our knowledge in this field is too limited in many cases.

A comparison between different biomes gives an impression that the dominant community type in one of them is often more or less similar to a minor one in another. So the dominant tundra communities resemble the forest zone heaths and bogs, the boreal coniferous forests remind one of more southern seral coniferous forests, the zonal steppes are reminiscent of dry meadows, while the deserts look like early xerosesal communities of

less arid regions. In general, the landscape-dominating communities in more harsh environments resemble certain ones in more favourable areas occupying a successional position prior to the dominant community. Certainly, there are many differences and those similarities may well be superficial in many cases; however, they are too widespread and regular to be purely accidental. The ecological successions originated from an imbalance between production, on the one hand, and consumption and destruction, on the other, in seral communities (Vakhrushev & Rautian 1993). The losses of the surplus seral production is the cost of reaching the intrinsically balanced and stable final (climax) stage by the system. The stability of climax is possible due to its complex functional organisation effectively controlling the main abiotic environmental variables. Such highly regulatory capacity is unattainable at earlier stages. However, both the climax and the previous successions are the products of evolution of co-adaptations between the co-existing populations. An optimisation of the rate between the climax stability and its successional costs would be an important factor of the successional system evolution (phylogenogenesis).

The acquiring of co-adaptations between two more populations of different species is possible when their common presence is highly predictable. This predictability decreases in small patches where the species turnover rate is high according to the well-known MacArthur and Wilson's (1967) island biogeography model. As a result, the interactions within more extensive communities would tend to become more specialised than in more localised and sporadically distributed ones. Furthermore, larger continuous areas support more diverse assemblages allowing more effective regulation of the ecosystem matter and energy turnover. So, it may be hypothesised that the landscape-dominating subclimaxes would have a tendency to evolve towards true climaxes while the climaxes would tend to miss their regulatory capacity when their area becomes too small. As a result of climax stages top-down the successions (due to the former climax stage loss and its replacement by a new one originating at the base of a former seral stage spatially expanded as the subclimax) would occur when certain subclimaxes remain constantly widespread throughout the area at the evolutionary time scale. This process of succession shortening from the top which may be called succession pruning would explain the biome pattern mentioned above.

#### **The Grassland Biomes**

The origin and history of some biomes seem to be in agreement with this hypothesis. The grassland biome provides an example. It has been discussed in detail in an



earlier paper (Zherikhin 1993), which is briefly summarised here.

There are some grass-dominated communities in nearly all modern successional systems, except those of some extremely arid or cold deserts. As a rule, they are intrinsically unstable and occupy relatively small patches of seral wet and dry meadows within undisturbed natural landscapes. They accumulate their surplus primary production in the form of a dead grass cover inhibiting grass regeneration but may be stabilised by exogenous disturbances removing the accumulated mortmass, especially by fires at drier sites or flood flows in floodplains. In anthropogenic environments grasslands managed by regular fires or mowing often become the landscape-dominating communities. There are also natural landscapes dominated by grasslands in different temperate and warm regions, mostly semi-arid, and the past existence of a cold grassland biome (the tundra-steppe) is well documented paleontologically. At least some natural grasslands are intrinsically stable and maintained mainly by mega- and mesoherbivores together with coprophages and detritivores. The rate of primary production consumption is extremely high, reaching 30–45% per year (occasionally even 60%) while its average rate in terrestrial communities is about 10% (Crawley 1983). Because the consumption values are estimated mostly for herbivorous mammals, they could be underrated: besides this key herbivorous group there are also important invertebrate herbivores, such as grasshoppers. All major grassland herbivores (ungulates, rodents and grasshoppers) are able to switch from herbivory to detritivory when the available grass biomass is decreasing; this is an important community-level regulating mechanism maintaining the biomass/mortmass balance. In this way they supplement the specialised detritivore guild, which is also diverse and effective in both temperate and hot grasslands. The guilds of mega- and mesoherbivores are well co-adapted and can mutually compensate the consumption rate fluctuations connected with occasional oscillations of consumer densities. There is also a high degree of co-adaptation between the herbivores and their major food-plants, the grasses, which are not only resistant to natural grazing but even show a positive regeneration response to it (McNaughton 1985).

Another key guild is that of the coprophages, which is also remarkably effective, rapidly removing up to 80–90% of the faeces produced by mega-herbivores (Fincher 1981). The crucial importance of dung consumption in pasture ecosystems is illustrated by well-known cases of pasture collapses induced by a severe dung fouling when the native coprophage guild is either ineffective (as in Australia) or suppressed by some drugs used in veterinary like Ivermectin (Lumaret et al. 1993). The guilds of coprophages and necrophages are also well co-adapted with the native mega-herbivore guild. Other functional blocs of the system are likely to be somewhat less important but not less co-adapted; for instance, the tumble-weed life form characteristic of many steppe

communities occurs in different herbs unpalatable to the major grazers and is adapted to a self-removing of their mortmass (Alekhin 1939). The rapid turnover of above-ground mortmass leads to the nutrient accumulation in soil. The high fertility of the steppe soils is well-known. The savanna soils are less fertile, but this is probably a consequence of the restriction of modern savannas to the strongly eroded ancient land masses which are, in general, poor in nutrients. When compared with the forest soils of the same regions, savanna soils show relatively high fertility (Bell 1982).

So the natural landscape-forming grasslands seem to be the true intrinsically stable climaxes (as defined by Zherikhin, this issue). Their intimately co-adapted structure is generally similar in different regions although there are important biogeographic differences in the taxonomical composition of some key blocs. This structure is certainly a result of a long-time history of co-existence of the major community components. The paleontological data, although rather fragmentary, throw some light on this history.

There are no well-grounded studies of treeless biomes which may have existed before the mid-Cretaceous angiosperm expansion. Although some authors discuss Mesozoic 'steppes' or 'savannas', such statements are not based on an analysis of a possible type of ecosystem turnover. The present state of knowledge suggests that the possibility of the existence of herbaceous climaxes dominated by some kinds of pre-angiosperm vegetation (for example, ferns or horse-tails) cannot be accepted or rejected with certainty. There are some modern grasslands managed by non-mammalian herbivores such as birds (Kishchinsky & Zlotin 1979; Bazely & Jeffries 1989) and giant turtles (Merton et al. 1974; Crawley 1983), but they are dominated by a gramin and sedges, which may be originally adapted to mammal grazing and the regulating capacity of herbivores here seem to be relatively imperfect. After the angiosperm expansion, some dinosaur groups (first of all the Ceratopsida) demonstrated a rapid development of supposed adaptations to grazing on herbaceous vegetation; this may be related to the appearance of open herb-dominated landscapes in Central Asia and North America in the Late Cretaceous, but the biocenotic nature of those communities still remains unclear (Zherikhin 1993). Possibly, these landscapes were occupied largely by unknown herbaceous angiosperms other than gramin. They seem to disappear with the dinosaur extinction near the Mesozoic–Cenozoic boundary, and there is no evidence of such extensive open landscapes in the Early Paleogene up to the Mid Eocene.

The most ancient evidence for Cenozoic grassland landscapes has been found in South America. The oldest supposedly herbivorous mammals (the notoungulate family Archaeohyracidae) demonstrate the development of grazing adaptation during the Casamayorian and Mustersian stages of the Eocene, and another group, the



glyptodontids (Xenarthra), appear in the Mustersian (Simpson 1980). Palynological and paleosol data as well as finds of abundant fossilised dung beetle balls also indicate the presence of more or less widely distributed steppe-like landscapes in South America at least since the mid Eocene time (Andreis 1972; Van der Hammen 1983). This interdisciplinary set of data suggests a self-regulated grassland regime (Zherikhin 1993).

The long isolation of South America has prevented the dispersion of key mammal herbivores beyond it. As a result, in North America grassland landscapes originated independently. The oldest North American grazing ungulates known are of the Oligocene age, and there are also Oligocene grass finds including feather-grasses (Galbreath 1974; Webb 1977). Most groups of non-Neotropical grazing mammals are of North American origin though few of them have survived in the Nearctic until now. The same is true probably for many other open landscape inhabitants; interestingly, even the tsetse flies blood-sucking on the megaherbivores and now restricted to the Afro-tropical region are known in North America from as early as the Early Oligocene. Paleobotanical data indicate the rapid expansion and evolution of prairie grasses during the Miocene and the development of morphological adaptations to regular grazing (Thomasson 1979, 1985). The savanna paleosols with dung beetle balls are known in the Late Oligocene in South Dakota (Retallack 1984). Since the Miocene, North American ungulate grazers have invaded Asia and further into Europe and Africa where environment changes toward more open habitats are documented since the Late Miocene (Winkler & Jacobs 1993). Probably, this mammal invasion initiated an expansion of grassland biome. This was a complex process involving many native plant and animal taxa, but the main ecosystem organisation probably had formed under the key influence of North American invaders (Zherikhin 1993). There is also paleosol evidence of grassland landscape existence in the interior of Asia since the Early Miocene (Kasimov 1988). During the late Cenozoic drop in temperature the characteristic cold-adapted ('mammoth') megaherbivore fauna arose from the same major taxa in Eurasia and North America; it was restricted to a peculiar grassland landscape type called the tundra-steppe (Velichko 1973; Matthews 1976; Verkhovskaya 1988). The ecological structure of the tundra-steppe mammal taxocene was remarkably similar to the savanna one (Vereshchagin & Baryshnikov 1991). The extinction of this fauna near the Pleistocene/Holocene boundary coincides with the disappearance of this kind of landscape (Ukrainitseva 1984; Verkhovskaya 1988).

The third independent case of grassland origin is the Australian one where the late Neogene diprotodontid marsupials demonstrate evident adaptations for grazing and the development of grassland is palynologically documented since the Miocene (Archer 1981; Martin 1981). Unfortunately, the paleoenvironmental data is still scarce here.

There are some features common for all these examples. Firstly, a primary area of grassland landscape origin is always situated in a region of water or nutrient deficiency where the succession rates would be relatively low. Secondly, a forest vegetation dominated the area before a grassland expansion. The first appearance of grazers and other open landscape indicators in the fossil record is always preceded by some evidence of parklands with medium- to large-sized mammalian browsers. This herbivore guild is unable to maintain stable grassland communities but its activity partially inhibits the tree and shrub regeneration and thus may further decrease the succession rate favouring grass stages expansion within the landscape (Zherikhin 1993). Thirdly, with the disappearance of megaherbivores the grassland area decreases dramatically. An anthropogenic extermination of wild ungulates makes the grassland landscapes intrinsically unstable. As a rule, moderate domestic cattle grazing may replace the nature grazing as a regulating mechanism, but it is less efficiently self-regulated and desertification effects because of overstocking are common, indicating an insufficient co-adaptation level. On the other hand, an exclusion of cattle grazing in protected grassland areas leads in the absence of wild grazers either to a reforestation or to development of shrub communities replacing the grasses or, if there is no source of tree seeds, to a cyclic succession indicating the absence of intrinsically stable stages in the successional system. Another way to support grasslands in the absence of natural grazing is a controlled burning removing the grass litter; however, in this case high nutrient losses lead to decreasing soil fertility and subsequent degradation of the natural community.

The case of the cold-zone grasslands is especially indicative because the agricultural use of the land is very limited and therefore the natural trends are more evident than in warmer regions. Interestingly enough, the Holocene extinction of large mammals has not been accompanied by a large-scale extinction in any other group of the tundra-steppe biota except for a few insect taxa intimately connected to megaherbivores such as the dung beetles (Miller et al. 1981). For instance, the rather well-studied tundra-steppe insect assemblages from the Pliocene and Pleistocene deposits of north-eastern Siberia lack extinct species but contain a number of taxa now distributed in cold steppes far outside this territory (Kisselev 1981). The Late Pleistocene insect fauna of Byelorussia also contains abundant Siberian steppe taxa (Nazarov 1984) and some cold-adapted steppe species are found even in the British Isles, including the dung beetle *Aphodius holdereri* Reitt. now restricted to alpine grasslands of Tibet (Coope 1973). However, there is no single modern cold steppe area supporting the entire tundra-steppe insect assemblage: the species found together as fossils in the Kolyma Basin, for instance, are now restricted to different, and often remote areas such as Alaska, Central Yakutia, Mongolia, Altai Mountains, etc. (Kisselev 1981). A similar pattern also occurs among plants. There are a number of local modern 'islands' of



relict steppe vegetation in northern Asia as well as in northern North America but this vegetation is now not landscape-forming anywhere in these regions, and the systematic composition of the flora differs in different 'islands' (Yurtsev 1981). Possibly this is the result of cold steppe fragmentation when smaller remnants of the past vast zone could no longer support the former biodiversity level. Studies in this field would be of great importance for the problem of optimal planning of nature reserve areas. Probably no modern cold steppes are intrinsically stable. They have returned to their original seral state in boreal forest successional systems, and this might be the natural fate of any grassland biome after large herbivore extinction.

### **The Fire-Regulated Biomes**

The Mediterranean-type biomes provide another example of probable succession pruning. This biome type is distributed on infertile soils in subtropical to warm-temperate regions with summer drought; the landscape-forming vegetation is represented by sclerophyllous evergreen or wintergreen shrubs with or without open woodlands. The areas of Mediterranean-type biomes are restricted now besides the Mediterranean region itself to south-western North America, Central Chile, South Africa and southern Australia (Specht & Moll 1983). The rate of primary production consumption is low both in grazing and detritus-processing pathways because of the unfavourable seasonal precipitation. Primary production culminates during a relatively cold rainy season when the herbivore activity is suppressed by unfavourable and rather unpredictable weather conditions (Kummerow 1983). The tough leaves of dominating sclerophyllous shrubs adapted to water loss minimisation during the early dry season and a maximisation of the duration of the vegetational season are of very little nutritive value except for the early stages of their development (Morrow 1983). On the other hand, mortmass production peaks during a hot dry season when detritivore and decomposer activity is low, especially in the litter stratum (Poinsoot-Balaguer 1985). Thus, the surplus unconsumed production is accumulated in the form of a coarse litter composed mostly of unpalatable dead leaves (Read & Mitchell 1983).

This turnover type with a large amount of accumulating mortmass is characteristic in general for seral communities and would indicate a subclimax nature of the landscape-forming communities. Indeed, the Mediterranean-type biomes are maintained by periodical fires rapidly mineralising the litter, and become unstable when the fires are excluded for several dozens of years (Recher & Christensen 1981; Huntley 1984; Keeley et al. 1986). However, in the Mediterranean-type biomes the fire is not an accidental disturbance event: it is not only highly predictable but its very predictability is determined and regulated by the community itself. The more the accumulated dry litter volume the more the probability of fire increases. Thus, the process is self-regulated though

its regulating mechanism seems to be rather primitive. Any subclimaxes are maintained by some predictable disturbances; but typically they cannot influence their own causes, they are passively regulated from outside. In fact, fire in Mediterranean-type biomes is often a biotic phenomenon compensating for low biological decomposition rates. In many cases plant tissues are remarkably rich in ether oils and other highly inflammable substances and poor in water content. The biota is well-adapted to fire, and besides numerous opportunistic adaptations raising the fire tolerance there are also some specialised adaptations making populations fire-dependent rather than simply fire-tolerant. For instance, the fruits of many Australian and South African Proteaceae possess thick lignified walls and need heating for their dehiscence and seed dispersal (Recher & Christensen 1981). Some Californian chaparral pines show a remarkable parallel: their cones are normally glued with resin which melts under heating so allowing the dispersion of seeds (Zedler & Zammit 1989). The chemical composition of seeds is also noteworthy and in this respect many Proteaceae seeds are rich in nitrogen and phosphorus but extremely poor in potassium, calcium and magnesium (Stock et al. 1990). It is certainly an adaptation to infertile soils, but this kind of adaptation would be effective only when seed dispersal is well synchronised with fires enriching the soil with ash. I believe further examples of fire-dependence will be discovered in Mediterranean-type biomes, especially in South Africa, Australia and California where they seem to be most stable. In effect, one may say that this is a peculiar case of co-adaptation between the biota and biotically-regulated natural fires. The nitrogen losses during a fire may be extremely high, but they are compensated for by widespread nitrogen fixation (Lamont 1982; Rundel 1983). Thus, naturally fire-regulated landscape-forming communities would be regarded as the primitive climaxes or, at least, as a transitional link between the typical subclimaxes and true climaxes. However, in many cases the modern Mediterranean-type landscapes are clearly anthropogenic as in the most part of the Mediterranean region where forest communities dominated by evergreen oaks represent the natural climax (Shmida 1982; Lücke 1984; Pons 1984, 1985; Deil 1989; Havel 1990; Vernet 1990; Wojterski 1990).

Paleontological data on the history of the Mediterranean-type biomes are summarised by Axelrod (1975, 1989), Axelrod and Raven (1978), Deacon (1983), and Zherikhin (in press). They are even more fragmentary than in the case of grasslands but seem to be in accordance with the pruning hypothesis. Although sclerophyllous angiosperms were rather diverse in the warm climatic belts by the Late Cretaceous, for a long time they remain likely as the components of dense forests resembling the modern Canarian laurisilva. Even now many plant taxa typical for Mediterranean-type communities are represented also in closed woodlands, mostly as understorey components. So, the understorey of Black



Sea coastal forests in Turkey includes ilex, myrtle, laurel and other Mediterranean shrubs (Shmida 1982) as well as the understorey of various Californian forests - a number of chaparral dominants (Griffin 1978; Axelrod 1989). A peculiar combination of plant taxa now characteristic for Mediterranean-type landscapes and wet forests is represented in Late Cretaceous and Paleogene pollen assemblages in southern Australia (Dettmann & Jarzen 1991). The oldest evidence of Mediterranean-type landscapes are of the Miocene or (in South Africa), possibly, of a late Paleogene age.

Hence, the modern Mediterranean-type biomes are probably relatively young. The regulation by natural community-controlled fires likely represents an early evolutionary stage of a climactization of subclimaxes in the course of succession pruning. At subsequent stages of the process other stabilisation mechanisms would appear. Possibly this later evolutionary stage is represented by some modern Australian eucalypt woodlands. They are effectively fire-regulated (Mount 1964; Recher & Christensen 1981), but there are also a diverse and abundant fauna of primary consumers (Ohmart & Edwards 1991). The rate of leaf consumption by herbivores is remarkably high in comparison to other forest communities, reaching 40-50% of their production in some cases (Journet 1981; Fox & Morrow 1983, 1986; Morrow & Fox 1989), and detritivore activity both in litter and soil is high in comparison to typical Mediterranean communities (Plowman 1979; Pressland 1982). The regulatory role of consumers is consequently sufficient, with the diverse and complex co-adaptive biotic interactions within the ecosystem which are only partially recognised at present (Springett 1978; Silander et al. 1985; Braithwaite 1990). The phenology of primary production differs from typically Mediterranean ones. There are many dominant plant species with summer vegetation (Specht 1973), and the litter production is less uneven (Pressland 1982). As a result, the consumer activity is also more evenly seasonally distributed (Majer & Koch 1982). So, fire-regulated eucalypt communities seem to be more phylogenetically advanced than the Mediterranean-type communities elsewhere; however, the South African fynbos and especially the South American matorral ecosystems are still insufficiently studied, and more co-adapted interactions may be detected here in future. On the other hand, some modern Mediterranean-type biomes may have lost their past specialised regulating mechanisms because of the isolation effects in the Quaternary when their areas in many regions had fluctuated at a rather large scale (Deacon 1983; Pons 1984; Vernet 1990). In any case, an advanced evolutionary level of eucalypt forests and woodlands is unlikely to be connected with their ancient age: there are no well-documented fossil eucalypt finds before the Oligocene-Early Miocene (Deacon 1983).

If the succession pruning hypothesis is correct, fire regulation would be widespread because of its relative simplicity. The past fire-regulated biomes may be

detected paleoecologically at the base of regular fossil fire evidences. Unfortunately, the available data are scattered in literature and unsystematised. However, the regulation by fires is really a common phenomenon as indicated by the fact that modern naturally fire-regulated communities are far from being restricted to the Mediterranean climate regions. In particular, the boreal coniferous forests are maintained by natural fires in many cases (Bormann & Likens 1979; Schowalter et al. 1981; Van Cleve et al. 1983; Baker & Veblen 1990). Here, again, an unconsumed and slowly decomposing dry litter is accumulating, and the community regeneration is hampered by it. A fire destroys the dense litter stratum and facilitates young growth establishing. The overstorey trees are relatively fire-tolerant, while the understorey often includes easily inflammable shrub species such as the ledum in larch taiga forests in Central and East Siberia. The abundance of such understorey species benefits surface fires and prevents more destructive crown ones. An abundant post-fire regeneration forms the even-aged forest stands which are characteristic of the boreal zone. The outbreaks of destructive insect pests in over-matured stands is another important mechanism maintaining the peculiar boreal forest dynamic pattern (Amman 1977; Werner & Holsten 1983; Veblen et al. 1991), and the fire and insect effects seem to be rather well concerted at least in some cases (Schowalter et al. 1981; Baker & Veblen 1990). Both phenomena are naturally correlated with an accumulation of large amounts of debris and give these types of communities a characteristic wave-like pattern of dynamics. Their long-term exclusion often leads to a replacing of conifers by hardwood stands in boreal-nemoral ecotones or in mountain forests. In warmer regions the coniferous forests are restricted to seral habitats, and their landscape-forming state in the boreal zone is probably one more case of the succession pruning.

### Other Possible Cases of Pruning

Thus, both the grassland and fire-regulated biomes seem to have originated by a pruning of successional systems formerly crowned with forest climaxes. The pruning process is initiated by an expansion of subclimaxes due to the succession rate decreasing because of an environmental limitation of primary production rates. The limiting factors may be different: the grasslands and shrub heathlands are expanding in areas with a water and/or nutrient deficiency whereas the boreal forests are developing in cold temperate regions where production rate is limited mostly by temperature and solar radiation. Consequently, the nature of expanding communities is also different, with originally meso- or hydrosereal ones dominating in moist cold temperate and xerosereal ones in dry landscapes. A progressive development of self-regulation mechanisms based on co-adaptations within the landscape-forming subclimaxes leads to their climactization while the former climaxes gradually lose their stability. In more extreme environments where the limitation is especially severe further succession pruning



processes would occur. In arid regions this is the probable way of desert biome origin. According to paleontological data, this type of modern biome is likely to be even younger than modern grasslands or Mediterranean-type bushlands which is in accordance with the hypothesis of continuous pruning. The largest modern deserts have expanded in the Holocene only when barren lands have gradually replaced the savannas or steppes, which existed formerly in these territories; the Sahara is the best known example (Wickens 1984). The age of other deserts is also young, late Neogene to Quaternary, with a very recent major expansion (Bakker van Zinderen 1975; Axelrod 1979; Bykov 1989). The self-regulation capacity in modern desert communities seems to be rather weak and they probably still keep their subclimax or permanent cyclic successional cycles (MacMahon 1980; Mathon 1982). The co-adaptation set is remarkably weak, which is especially apparent in comparison with the high diversity of striking adaptations peculiar to abiotic environments. This situation may be explained easily if the members of a system have a long history of specialisation in pioneer xeroseral environments of other systems (such as dunes or solonchaks) but only a short evolutionary experience of interactions with one another. However, there is a biotic agent which may maintain desert habitats, at least principally, namely digging animals. Their activity is of great and diverse importance: they remove the surface litter and renew barren surface substrates preventing soil accumulation, distribute nutrients over a deep soil profile, create the shelters with sufficiently more mild microclimate which are exploited by a great number of other organisms, etc. (Gutterman & Golan 1990). This lifestyle is widespread also in less pruned grassland systems, and its significance seems to increase in the driest, short-grass types and early successional stages (Platt 1975; Coffin & Lauenroth 1988; Peart 1989; Martinsen et al. 1990; Dean & Milton 1991).

The boreal successional systems are also affected by further pruning in more harsh environments, where their early hydrosere began forming the tundra landscapes. This biome is certainly of latest Cenozoic origin and demonstrates the same features as the desert one: the successions are weakly organised and cyclic (MacMahon 1980; Tikhomirova & Razumovsky 1988), and co-adaptive biotic interactions are weakly developed (Tishkov 1992). The existence of open forest-tundra communities instead of true tundra in high Arctic as late as in the Pliocene is now well documented (Matthews 1973; Bennike & Boecher 1990). However, the ancestors of the modern tundra taxa may have been specialised to sereal heath and bog habitats as well as to severe alpine environments well before the first appearance of zonal tundra landscapes. Their dispersion in the Pleistocene over the vast territories has led to the formation of new niche combinations which are the field of co-adaptation. Repeating oscillations of tundra and tundra-steppe landscapes during the glaciation/deglaciation cycles with expansion of the former in moister interglacials and the

latter in the drier glacials have complicated an acquiring of stable co-adaptations. The self-regulation capacity is limited, but an interesting parallel to fire-regulation is noteworthy: a dense moss cover strongly limits soil thawing in summer so that the permafrost upper limit is partially biotically controlled. A similar situation exists in subarctic larch forests in Siberia where a dense needle litter plays the same thermo-insulating role. In both modern desert and tundra successional systems there are no definite stable final stages and instead of it, a stable mosaic type is maintained; the same is true for some types of coniferous forests, especially in montane areas.

In the Antarctic region where the Cenozoic glaciation began much earlier, the tundra-like open communities would have a longer history. Unfortunately, our knowledge on the Neogene biota of the Antarctic continent is still too limited and its biocenotic organisation is virtually unknown.

Hence succession pruning seems to be a widespread mechanism of biome diversification. Probably it also operates within the same biome. The successional systems of East European hardwood forests described by Razumovsky (1981) demonstrate clearly a shift of successional position of different oak species in relation to latitude: in warmest Krym and eastern Caucasus regions *Quercus robur* occupies late hydrosere habitats, *Q. petraea* the late mesosere, and *Q. pubescens* is the edifier of climax; northwards the latter species disappears and the climax stage is shifted to *Q. petraea* forests while *Q. robur* retains its hydrosere position; further to the north where the latter becomes the only oak species it dominates the climax forests. In the latter area the late hydrosere is dominated by the Norwegian spruce *Picea abies* which becomes the climax dominant northwards, in the boreal zone. Razumovsky has mentioned this regular pattern of northward succession shortening in his unpublished manuscript on florogenesis communicated after the author's death by A. P. Rasnitsyn at the workshop on vegetation dynamics in the Botanical Institute in St Petersburg in 1992. He considered this phenomenon (under the name of cryogenesis) related to colder climatic conditions; in my view, the cryogenesis of Razumovsky is a special case of succession pruning.

### General trends of the process

A comparison among the above cases permits some common trends to be recognised. Probably the most important point is a landscape shift connected with phylogenetically-induced changes of community tolerance limits. Certainly, there were moister and drier regions in the early Paleogene, before the beginning of grassland and bushland expansion. As there is no evidence of open landscapes, dry woodlands would exist at this time even in the most arid regions. But, if so, why have they been later replaced by treeless landscapes? A progressive drying hypothesis is the most common suggestion. However, the evolution of biota provides



another or, a possibly complementary answer. Surely, the limits of water stress tolerance depend upon other stress factors, and the activity of browsers is one of them. Thus, after the extinction of large-sized herbivorous reptiles and before the appearance of large browsing mammals, the biotic pressure on tree vegetation would be reduced, and the vegetation distributional pattern along the moisture gradients would be less. However, less dense woodlands in drier regions make possible a mammal evolution toward the herbivory in the larger size class: when this possibility had been realised, the situation began to change. The tree density had begun to decrease in most dry environments, and the replacing of woodland communities by earlier successional treeless stages would be a consequence. In phytocenogenetical terms (Zherikhin, this issue), a specio-genetic event (mammal evolution) initiated the secondary esogenetic effects (changes in a successional stage equilibrium). The woodland area was gradually diminishing up to a new equilibrium level determined by browser activity, decreasing soil moisture at more open sites, changing light regime, and other associated effects.

However, an expansion of early successional stages including grasslands has opened a new possibility for mammal evolution: the expansion of grazers has originated within the system. When this possibility, in its turn, had been realised (one more specio-genetic event), the equilibrium was disrupted again. The woodland area has reduced further while in expanded treeless communities two alternative ways for evolution of dominant plant taxa have become available: one toward an adaptation for mammal grazing and another to an increasing protection against it. The former is leading to a pasture type community and has been actualised in stable grasslands; the latter leads to a detrite community type and has been actualised in Mediterranean shrublands. At the same time, digging mammals were evolved as a component of treeless communities, and their evolution has changed the equilibrium state in driest habitats once more. There are many other taxa besides plants and mammals which have been involved in co-evolutionary interrelations, and some of them were of great importance, like the above-mentioned coprophagous and saprophagous insects in pasture ecosystems or herbivorous insects in dry eucalypt forests.

Hence, after the appearance of browsers, parklands would tend to expand due to their pressure, the grazers then initiate their replacement by grasslands and further parklands shift into formerly forested regions, the diggers continue the process, provoking a biogenous desertification in dry steppe regions and additional shifts of other landscape types. Physiographical changes such as climatic shifts connected to the global distribution of land masses and sea current pattern should influence this process significantly but precipitation and evaporation values and ratio depend on forested land patterns and thus may be changed also biotically at a rather wide scale. Thus, both the steppification and desertification are

complex processes, with multiple iterative interactions between biological (phytocenogenetical) and physiographical events. In general, physiography changes may facilitate or inhibit certain potentially possible phylogenetic trends but cannot create them. They operate as triggers of evolutionary processes, which have been already prepared biologically rather than as their ultimate causes. They are provokers of organic evolution but not its initiators. So, biological and biocenological effects of any physiographic event depend on the presence or absence of taxa which are potentially able to seize the opportunity given by it. It would explain why there are no obvious general correlations between the magnitude of physiographic and evolutionary events.

Another general feature of pruning is the frequency of parallels between independently evolved systems, which are evident from the cases mentioned above. However, the parallel phytocenogenesis is limited by possible dissimilarities in specio-genetic potentials between different areas or times. For instance, before a discovery of evidence for adaptations to continuous grazing in pre-angiosperm fossil vegetation a generalisation about the steppification pattern on Mesozoic and Paleozoic would be premature. On the other hand, the physiographic factors of pruning are also variable at the geological time scale. For example, a peculiar type of polar zone existed in the past: the climate was temperate and the seasonal light deficiency would be the key factor limiting primary production and succession rates. It may be hypothesised that in this case the pruning would support hydrosereal stages as the landscape-forming ones.

The role of consumers in climax communities should be stressed. In general, they are not absolutely necessary for a biocenotic system functioning unlike producers and destructors; however, their presence is sufficient for regulation, and their regulatory capacity seems to increase in the course of their evolution as well as in the course of phytocenogenesis of different successional system types. From this point, the appearance of consumer stabilising successions at the stage of primitive groupings as man makes by its agriculture is not an evolutionary accident but a further and probably unavoidable step in this natural process.

If succession is treated as a peculiar type of ontogenesis (Zherikhin, this issue), the succession pruning would be regarded as a phytocenogenetic parallel to neoteny. In both cases the number of developmental stages preceding the final stage is decreasing and the cost of maturation is consequently minimised. Both the pruning and neoteny are widespread in relatively harsh environments where this minimisation is especially profitable; in more favourable situations a risk associated with the former mature stage loss would exceed the advantage of development shortening.



## Conclusions

The pruning hypothesis generates a number of predictions which may be useful in paleontology. In particular, it allows a prediction of a landscape community dominance in poorly studied areas on the base of successions recognised in other regions. An inverse problem is the prediction of seres poorly represented in the fossil record; for example, the general set of taxa exploiting xeroseal habitats in mesic zones can be predicted on the base of data on landscape-forming communities in dry regions. An effect of climatic regime stability on phylogenogenesis may be also predicted: the epochs of repeating drastic climatic changes such as late Cenozoic would favour a rapid biome diversification by pruning but prohibit climactization processes in landscape-forming subclimaxes because of their fluctuating while more climatically stable situations would be characterised by less diversified biomes which are, however, dominated mostly by their own true climaxes.

## References

- Alekhin, V. V. 1939, 'Some considerations about the tumble-weed life form', in *Prezidentu AN SSSR okad. V.L. Komarova k 70-letiyu so dnya rozhdeniya i 45-letiyu nauchnoi deyatel' nosti (To the President of the USSR Academy of Sciences Academician V.L. Komarov's 70th Birthday and 45 Years of His Scientific Activities)*, ed. AN SSSR, Moscow-Leningrad, pp. 97-107 (in Russian).
- Amman, G. D. 1977, 'The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession', in *The role of arthropods in forest ecosystems*, ed. W. J. Mattson, Springer, Berlin, pp. 3-18.
- Andrés, R. R. 1972, 'Paleosuelos de la Formación Masters (Eoceno medio), Laguna del Mate, Prov. de Chubut, Rep. Argentina', *Revista Assoc. Mineral., Petrol. Sedimentol. Argentina*, 3, pp. 91-97.
- Archer, M. A. 1981, 'A review of the origin and radiations of Australian mammals', in *Ecological Biogeography of Australia* vol. 3, ed A. Keast, W. Junk, The Hague, pp. 1435-1488.
- Axelrod, D. I. 1973, 'History of the Mediterranean ecosystem in California', in *Mediterranean Type Ecosystems: Origin and Structure*, eds F. di Castri & H. A. Mooney, Springer, Berlin, pp. 225-277.
- Axelrod, D. I. 1975, 'Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation', *Ann. Missouri Bot. Garden*, 12, pp. 280-334.
- Axelrod, D. I. 1979, 'Age and origin of Sonoran desert vegetation', *Occas. Pap. Calif. Acad. Sci.*, 132, pp. 1-74.
- Axelrod, D. I. 1989, 'Age and origin of chaparral', *Sci. Series Natur. Hist. Mus. Los Angeles County*, 34, pp. 7-19.
- Axelrod, D. I. & Raven, P. H. 1978, 'Late Cretaceous and Tertiary vegetation history of Africa', in *Biogeography and Ecology of Southern Africa*, ed. M. J. A. Werger, W. Junk, The Hague, pp. 77-130.
- Baker, W. L. & Veblen, T. T. 1990, 'Spruce beetles and fires in the nineteenth-century subalpine forests of Western Colorado, U.S.A.', *Arctic and Alpine Res.*, vol. 22 no. 1, pp. 65-80.
- Bakker van Zinderen, E. M. 1975, 'The origin and palaeoenvironment of the Namib desert biome', *J. Biogeogr.*, vol. 2 no. 2, pp. 65-73.
- Bazely, D. R. & Jeffries, R. L. 1989, 'Lesser snow geese and the nitrogen economy of a grazed salt marsh', *J. Ecol.*, vol. 77 no. 1, pp. 24-34.
- Bell, R. H. V. 1982, 'The effect of soil nutrient availability on community structure in African ecosystems', in *Ecology of Tropical Savannas*, eds B. J. Huntley & B. H. Walker, Springer-Verlag, Berlin, pp. 193-216.
- Bennike, O., & Boecher, J. 1990, 'Forest-tundra neighbouring the North Pole: plant and insect remains from the Plio-Pleistocene Kap Kobenhavn Formation, North Greenland', *Arctic*, vol. 43 no. 14, pp. 331-338.
- Bormann, F. H. & Likens, G. E. 1979, 'Pattern and process in a forested ecosystem', Springer, New York.
- Braithwaite, R. W. 1990, 'Australia's unique biota: implications for ecological processes', *J. Biogeogr.*, vol. 17 nos 4-5, pp. 347-354.
- Bykov, B. A. 1989, 'Evolution of Turan lowland desert ecosystems', in *Ekosistemnye issledovaniya: istoriko-metodologicheskie aspekty (Ecosystem studies: historical-metodological aspects)*, eds T. S. Beniaminso, A. I. Kafanov & E. I. Kolchinsky, Vladivostok, pp. 76-93 (in Russian).
- Coffin, D. P. & Lauenroth, W. K. 1988, 'The effects of disturbance size and frequency on a shortgrass plant community', *Ecology*, vol. 69 no. 5, pp. 1609-1617.
- Coope, G. R. 1973, 'Tibetan species of dung beetle from Late Pleistocene deposits in England', *Nature*, vol. 245, no. 5424, pp. 335-336.
- Crawley, M. J. 1983, *Herbivory. The dynamics of animal-plant interactions*, Studies in Ecology, vol. 10, Blackwell, Oxford.
- Deacon, H. J. 1983, 'The comparative evolution of Mediterranean-type ecosystems: A southern perspective', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 3-40.
- Dean, W. R. J. & Milton, S. J. 1991, 'Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites', *Afr. J. Ecol.*, vol. 29 no. 1, pp. 11-16.
- Deil, U. 1989, 'Contribution à l'étude des groupements secondaires du Haut Rif Central (Maroc). Comparaison avec quelques séries de dégradation de la végétation Ibérique', *Stud. botan.*, 8, pp. 79-90.
- Detmann, M. E. & Jarzen, D. M. 1991, 'Pollen evidence for Late Cretaceous differentiation of Proteaceae in southern polar forests', *Canad. J. Bot.*, vol. 69 no. 4, pp. 901-906.
- Fincher, G. T. 1981, 'The potential value of dung beetles in pasture ecosystems', *J. Georgia Entomol. Soc.*, 1, suppl. 1, pp. 316-333.
- Fox, L. R. & Morrow, P. A. 1983, 'Estimates of damage by herbivorous insects on Eucalyptus trees', *Aust. J. Ecol.*, vol. 8 no. 2, pp. 139-147.
- Fox, L. R. & Morrow, P. A. 1986, 'On comparing herbivore damage in Australian and north temperate systems', *Aust. J. Ecol.*, vol. 11 no. 4, pp. 387-393.
- Galbreath, E. C. 1974, 'Stipoid grass "seeds" from the Oligocene and Miocene deposits of northeastern Colorado', *Trans. Illinois State Acad. Sci.*, vol. 67 no. 3, pp. 366-368.
- Griffin, J. R. 1978, 'Maritime chaparral and endemic shrubs of the Monterey Bay region, California', *Madroño*, vol. 25 no. 2, pp. 65-81.
- Guterman, Y. T. & Golan, M. Garsani 1990, 'Porcupine diggings as a unique ecological system in a desert environment', *Oecologia*, vol. 85 no. 1, pp. 122-127.
- Haveh, Z. 1990, 'The role of fire in the co-evolution of Mediterranean man and landscapes', *Abstr. 5th Internat. Congr. Ecol.*, Yokohama, August 23-30, 1990, Yokohama, 176 pp.
- Huntley, B. J. 1984, 'Characteristics of South African biomes', in *Ecological Effects of Fire in South African Ecosystems*, eds P. de V. Booysen & N. M. Tainton, Springer-Verlag, Berlin, pp. 1-17.
- Journet, A. R. P. 1981, 'Insect herbivory on the Australian woodland eucalypt, *Eucalyptus blackleyi* M.', *Aust. J. Ecol.*, vol. 6 no. 2, pp. 135-138.
- Kasimov, N. S. 1988, *Geokhimiya stepnykh i pustynnykh landshaftov (Geochemistry of Steppe and Desert Landscapes)*, Moscow State University Press (in Russian).
- Keeley, J. F., Brooks, A., Bird, T., Cory, S., Parker, H., Usinger, E. 1986, 'Demographic structure of chaparral under extended fire-free conditions', *Calif. Water Resources Centre Univ. Calif. Davis Rept.*, no. 62, pp. 133-137.
- Kisselev, S. V. 1981, *Pozdnekainuozoiske zhestkokrylye Severo-Vostoka Sibiri (The Late Cenozoic Coleoptera of the Siberian North-East)*, Nauka Press, Moscow (in Russian).
- Kishchinsky, A. A. & Zlotin, R. I. 1979, 'The effect of geese grazing on vegetation cover (after the observation at the Chukotka Peninsula) Tezisy dokladov 7 Vsesoyuznoi zoogeograficheskoi konferentsii', *Proc. 7th All-Union Zoogeographic Conference*, Moscow, pp. 242-245 (in Russian).
- Kummerow, J. 1983, 'Comparative phenology of Mediterranean-type plant communities', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 300-317.



- Lamont, B. 1982, 'Mechanisms for enhancing nutrient uptake in plants, with particular reference to Mediterranean South Africa and Western Australia', *Botan. Revue*, vol. 48 no. 3, pp. 597-689.
- Lücke, H. 1984, 'Macchie und Garrigue Korsikas. Ökologische Grundlagen, Zusammensetzung, Verbreitung und Nutzung mediterran-insularer Pflanzenformationen', *Geobotanik*, vol. 5 no. 3, pp. 147-182.
- Lumaret, J. P., Galante, E., Lumberras, C., Mena, J., Bertrand, M., Bernal, J. L., Cooper, J. F., Kadiri, N., Crowe, D. 1993, 'Field effects of Ivermectin residues on dung beetles', *J. Appl. Ecol.*, no. 30, pp. 428-436.
- MacArthur, R. H. & Wilson, E. O. 1967, *The Theory of Island Biogeography*, Princeton Univ. Press.
- MacMahon, J. A. 1980, 'Successional processes: comparisons among biomes with special reference to probable roles to and influences on animals', in *Forest succession: concept and application*, eds. D. C. West, H. H. Shugart, D. W. Botkin, Springer, New York, pp. 277-304.
- McNaughton, S. J. 1985, 'Ecology of a grazing ecosystem: the Serengeti', *Ecol. Monogr.*, vol. 55 no. 3, pp. 259-294.
- Majer, J. D. & Koch, L. E. 1982, 'Seasonal activity of hexapods in woodland and forest leaf litter in the south-west of Western Australia', *J. Roy. Soc. West. Australia*, vol. 65 no. 2, pp. 37-45.
- Martin, H. A. 1981, 'The Tertiary flora', in *Ecological biogeography of Australia* vol. 1, ed. A. Keast, W. Junk, The Hague, pp. 391-406.
- Martinsen, G. D., Cushman, J. H., Whitlam, T. G., 1990, 'Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community', *Oecologia*, vol. 83 no. 1, pp. 132-138.
- Mathon, C. C. 1982, 'Le climax est une mouvante réalité mais son concept reste statique', *C. r. Soc. biogéogr.*, vol. 58 no. 3, pp. 111-116.
- Matthews, J. V. Jr. 1973, 'A preliminary list of insect fossils from the Beaufort Formation, McIghen Island, District of Franklin', *Geol. Surv. Canada Paper*, no. 74-1(A), pp. 203-206.
- Matthews, J. V. Jr. 1976, 'Arctic steppe — an extinct biome', *AMQUA Abstracts* no. 4, pp. 73-77.
- Merton, L. F. H., Bourn, D. M., Hnatiuk, R. J. 1974, 'Giant tortoise and vegetation interactions on Aldabra Atoll. I', *Inland. Biol. Conserv.* no. 9, pp. 293-304.
- Miller, S. E., Gordon, R. D., Howden, H. F. 1981, 'Reevaluation of Pleistocene Scarab beetles from Rancho La Brea, California (Coleoptera: Scarabacidae)', *Proc. Entomol. Soc. Wash.*, vol. 83 no. 4, pp. 625-630.
- Morrow, P. A. 1983, 'The role of sclerophyllous leaves in determining insect grazing damage', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 509-524.
- Morrow, P. A. & Fox, L. R. 1989, 'Estimates of pre-settlement insect damage in Australian and North American forests', *Ecology*, vol. 70 no. 4, pp. 1055-1060.
- Mount, A. 1964, 'The interdependence of the eucalypts and forest fires in South Australia', *Aust. Forest.*, no. 28, pp. 166-172.
- Nazarov, V. I. 1984, 'The reconstruction of Byelorussia landscapes based on paleontomological data (Quaternary)', *Trudy Paleontol. Inst. AN SSSR*, no. 205, pp. 1-96 (in Russian).
- Ohmart, C. P. & Edwards, P. B. 1991, 'Insect herbivory on Eucalyptus', *Ann. Rev. Entomol.*, no. 36, pp. 637-657.
- Peart, D. R. 1989, 'Species interactions in a successional grassland III. Effects on canopy gaps, gopher mounds and grazing on colonisation', *J. Ecol.*, vol. 77 no. 1, pp. 267-289.
- Platt, W. J. 1975, 'The colonisation and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie', *Ecol. Monogr.*, no. 45, pp. 285-305.
- Plowman, K. P. 1979, 'Litter and soil fauna of two Australian subtropical forests', *Aust. J. Ecol.*, vol. 4 no. 1, pp. 87-104.
- Poinsot-Balaguer, N. 1985, 'Comportement des microarthropodes du sol en climat méditerranéen français', *Bull. Soc. botan. France*, vol. 131 nos. 2-4, pp. 307-318.
- Pons, A. 1984, 'Les changements de la végétation de la région méditerranéenne durant le Pliocène et le Quaternaire en relation avec l'histoire du climat et de l'action de l'homme', *Webbia*, no. 38, pp. 427-439.
- Pons, A. 1985, 'La paléocologie face aux variations spatiales du bioclimat méditerranéen', *Bull. Soc. botan. France*, vol. 131 nos. 2-4, pp. 77-83.
- Pressland, A. J. 1982, 'Litter production and decomposition from an overstorey of Eucalyptus spp. on two catchments in the New England region of New South Wales', *Austral. J. Ecol.*, vol. 7 no. 2, pp. 171-180.
- Razumovsky, S. M. 1981, *Zakonomernosti dinamiki biatsenozov* (The Pattern of Biocenose Dynamics), Nauka Press, Moscow (in Russian).
- Read, D. J. & Mitchell, D. T. 1983, 'Decomposition and mineralisation processes in Mediterranean-type ecosystems and in heathlands of similar structure', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 208-232.
- Recher, H. F. & Christensen, P. E. 1981, 'Fire and the evolution of the Australian biota', in *Ecological Biogeography of Australia* vol. 1, ed. A. Keast, W. Junk, The Hague, pp. 135-162.
- Retallack, G. J. 1984, 'Trace fossils of burrowing beetles and bees in an Oligocene paleosol, Badlands National Park, South Dakota', *J. Paleontol.*, vol. 58 no. 2, pp. 571-592.
- Rundel, P. W. 1983, 'Impact of fire on nutrient cycles in Mediterranean-type ecosystems with reference to chaparral', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 197-207.
- Schowalter, T. D., Coulson, R. N., Crossley, D. A., Jr. 1981, 'Role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest', *Environ. Entomol.*, vol. 10 no. 6, pp. 821-825.
- Shmida, A. 1982, 'Mediterranean vegetation in California and Israel: similarities and differences', *Israel J. Botany*, vol. 30 no. 3, pp. 105-123.
- Silander, J. A. Jr., Fox, L. R., Trenbath, B. R. 1985, 'The ecological importance of insect frass: allelopathy in eucalypts', *Oecologia*, vol. 67 no. 1, pp. 118-120.
- Simpson, G. G. 1980, *Splendid Isolation. The Curious History of South American Mammals*, Yale Univ. Press (cited after the Russian translation 1983, Mir Press, Moscow).
- Specht, R. L. 1973, 'Structure and functional response of ecosystems in the Mediterranean climate of Australia', *Ecol. Studies*, vol. 7, pp. 113-120.
- Specht, R. L. & Moll, E. J. 1983, 'Mediterranean-type heathlands and sclerophyllous shrublands of the World: an overview', in *Mediterranean-type Ecosystems: The Role of Nutrients*, ed. F. J. Kruger, Springer, Berlin, pp. 41-65.
- Springett, B. P. 1978, 'On the ecological role of insects in Australian eucalypt forests', *Aust. J. Ecol.*, vol. 3 no. 2, pp. 129-139.
- Stock, W. D., Pate, J. S., Delfs, J. 1990, 'Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae', *J. Ecol.*, vol. 78 no. 4, pp. 1005-1020.
- Thomasson, J. R. 1979, 'Late Cenozoic grasses and other angiosperms from Kansas, Nebraska, and Colorado: biostratigraphy and relationships to living taxa', *Kansas Geol. Survey Bull.*, no. 218, pp. 1-68.
- Thomasson, J. R. 1985, 'Miocene fossil grasses: possible adaptation in reproductive bracts (lemma and palca)', *Ann. Missouri Bot. Garden* vol. 72 no. 4, pp. 843-851.
- Tikhomirova, A. L. & Razumovsky, S. M. 1988, 'The particularities of successional system functioning at the Extreme North', in *Biologiya pochv Severnoi Evropy* (Soil Biology in Northern Europe), Nauka Press, Moscow, pp. 59-68 (in Russian).
- Tishkov, A. A. 1992, 'The herbivorous mammals and successions of tundra ecosystems', in *Tsenoticheskie vzaimodeistviya v tundrovyykh ekosistemakh* (Cenotic interactions in tundra ecosystems), ed. Y. I. Chernov, Nauka Press, Moscow, pp. 28-38 (in Russian).
- Ukrainceva, V. V. 1984, 'The importance of studies of Siberian fossil megaherbivore food content for paleogeographic reconstructions', *Botan. Zhurnal*, vol. 69 no. 7, pp. 905-915 (in Russian).
- Vakhrushev, A. A. & Rautian, A. S. 1993, 'A historical approach to the community ecology', *Zhurnal Obshchei Biologii*, vol. 54 no. 5, pp. 532-555 (in Russian).
- Van Cleve, K., Dymess, C. T., Viereck, L. A., Fox, J., Chapin, F. S., III, Oechel, W. 1983, 'Taiga ecosystems in Interior Alaska', *BioScience*, vol. 33 no. 1, pp. 39-44.
- Van der Hammen, T. 1983, 'The palaeoecology and palaeogeography of savannas', in *Tropical savannas*, ed. F. Burliere, Elsevier, Amsterdam, pp. 19-35.



- Veblen, T. T., Hadley, K. S., Reid, M. S., Robertus, A. J. 1991, The response of subalpine forests to spruce beetle outbreak in Colorado, *Ecology*, vol. 72 no. 1, pp. 213–231.
- Velichko, A. A. 1973, *Prirodnyi protsess v pleistocene* (The nature process in Pleistocene), Nauka Press, Moscow (in Russian).
- Vereshehagin, N. K. & Baryshnikov, G. F. 1991, 'The ecological structure of the "mammoth fauna" in Eurasia', *Ann. zool. fenn.*, vol. 28 nos. 3–4, pp. 253–259.
- Verkhovskaya, N. B. 1988, 'Mammoth ecosystems and the causes of their disappearance', *Zhurnal Obshchei Biologii*, vol. 49 no. 1, pp. 70–83 (in Russian).
- Vernet, J.-L. 1990, 'Man and vegetation in the Mediterranean area during the last 20,000 years', in *Biological Invasions in Europe and Mediterranean Basin*, Elsevier, Dordrecht, pp. 161–168.
- Webb, S. D. 1977, 'A history of savanna vertebrates in the New World Part 1: North America', *Annual Rev. Ecol. System*, no. 8, pp. 355–380.
- Weischet, W. 1978, 'Die ökologisch wichtigen Charakteristika der kühlgemäßigten Zone Südamerikas mit vergleichenden Anmerkungen zu den tropischen Hochgebirgen', in *Geocological Relations between the Southern Temperate Zone and the Tropical Mountains. Proc. Symp. Internat. Geogr. Union Comm. High-Altitude Geocology*, Mainz, 1974, ed. by Carl Troll and Wilhelm Lauer, Steiner, Wiesbaden, pp. 255–279.
- Werner, R. A. & Holsten, E. H. 1983, 'Mortality of white spruce during a spruce-beetle outbreak on the Kenai Peninsula in Alaska', *Canad. J. Forest Res.*, no. 13, pp. 96–101.
- Wickens, G. E. 1984, 'Flora', in *Key Environments: Sahara Desert*, ed. J. L. Cloudsley-Thompson, Pergamon Press, Oxford, pp. 67–75.
- Winkler, A. J. & Jacobs, L. L. 1993, 'The fossil mammals of Africa', *Abstr. 6th Internat. Theoretical Congr.*, Sydney 4–10 July 1993, Sydney, pp. 321–322.
- Wojterski, T. W. 1990, 'Degradation stages of the oak forests in the area of Algiers', *Vegetatio*, vol. 87 no. 2, pp. 135–143.
- Yurtsev, B. A. 1981, *Reliktovye stepnye komplekсы Severo-Vostochnoi Azii* (The relic steppe assemblages of North-East Asia), Nauka Press, Novosibirsk (in Russian).
- Zedler, P. H. & Zammit, C. A. 1989, 'A population-based critique of concepts of change in the chaparral', *Sci. Series Natur. Hist. Mus. Los Angeles County*, no. 34, pp. 73–83.
- Zherikhin, V. V. 1993, 'The nature and history of grassland biomes', in *Stepi Evrazii: problemy sokhraneniya i vosstanovleniya* (Steppes of Eurasia: Conservation and Restoration Problems), ed. Z. V. Karamysheva, St Petersburg, Moscow, pp. 29–49 (in Russian).
- Zherikhin, V. V. 1994, 'The genesis of grassland biomes', in *Ekosistemnyye perestroiki i evolyutsiya biosfery 1* (Ecosystem Restructures and the Evolution of Biosphere), eds A. Y. Rozanov and M. A. Semikhatov, Nedra Press, Moscow, pp. 132–137 (in Russian).
- Zherikhin, V. V. (in press 1996), 'The nature and history of Mediterranean-type biome', in *Ekosistemnyye perestroiki i evolyutsiya biosfery* (Ecosystem Restructures and the Evolution of Biosphere) 3, eds A. Y. Rozanov and M.A. Semikhatov, Moscow (in Russian).

### 3.3 Density, Diversity and a General Model of Ecosystem Evolution

Valentin Krassilov

The late Professor D. Ager has argued that the Panda, a WWF heraldic species, is not worth protecting, for, being a slow reproducing, slow moving and dietarily fastidious animal, it is doomed by evolution itself (Ager 1991). Conservationists feel differently, however, although they seem lacking any scientific arguments for caring for the Panda. The situation resembles the evolutionist versus humanitarian controversies of the 1870s–1880s when Tolstoy (also Turgenev, Flaubert, Daudet, Dostoevsky, Meredith, Bourget, etc.) tried, on sentimental grounds alone, to protect people from selectionism. They have failed and the political ‘solutions’ of the controversy have been left to the Nazi and Marxian rulers.

Evidently, our notions of what adaptation is and how it is achieved lay at the core of the problem. In essence, the Darwinian model of adaptation held that a population ( $P$ ) starting at a particular variation ( $V_1$ ) and fitness ( $F_1$ ) arrives, through selection of the constituent gene frequencies, at a different variation ( $V_2$ ) resulting in a superior fitness ( $F_2$ ) manifested through the population growth ( $dP$ ):

$$P(V_1F_1) - (\text{selection}) \rightarrow P + dP(V_2F_2)$$

If  $dP > 0$  then

$$F_2 > F_1$$

To this R. Fisher has added an assumption that the larger the  $V_1$  the faster the increase in  $F$  (Edwards 1995).

This model does not explain a progression from the lower forms of life to the higher, nor the origin of species nor, for that matter, any other natural phenomena of general interest. Rather, it succeeded in separating natural science from natural human interests. But this is a side issue at the moment, for we are interested primarily in population growth as a measure of fitness. In the Darwinian model any trait actually or potentially enhancing population growth is considered as increasing fitness, thereby an evolutionary achievement. Incidentally, since plant communities produce more seeds under heavy grazing or browsing, the plant fitness must be increased by herbivory (McNaughton 1986; Belsky 1986). How good to be eaten! Despite the constantly repeated claims to the contrary, the logic of the Darwinian model is falsifiable and even readily so. As is discussed later in this paper, a positive  $dP$  disrupts density ratios of a balanced ecosystem and is eventually deleterious for the growing population itself — a fitness loss rather than a gain. In the alternative model population growth is interpreted as an evolutionary failure for only the maladapted organisms rely on sheer numbers for their survival.

In organisms of high reproductive potential population growth is typically regulated by a negative environmental feedback inflicting the high amplitude density fluctuations (e.g. in drosophilid flies, tundra rodents, etc.). Such organisms tend to surpass their sustainable density ( $D_s$ ) by a certain number of individuals constituting a redundant density component ( $D_r$ ), which then is sacrificed to environmental hazards serving as a buffer from complete extinction. The necessity to produce  $D_r$  render these populations over-consumptive and destructive to their environments, thereby an adaptation failure. On the other hand, organisms arriving at a sustainable density typically obtain an innate control of their reproductive potentials (e.g. hatch size regulation negatively correlated with life expectancies in birds or even in wasps (Mangel & Clark 1988), or estrus periodicity regulation in mammals, notably in the Panda), thus minimising the redundant component of their populations. Consequently,  $D_r$  can serve as a negative measure of fitness.

The ‘psychology’ under the Darwinian model above seems to have been inherited from those pioneer herdsmen who pleaded in their prayers for their progeny being multiplied as sand in the desert. Recently social priorities have shifted from growth to sustainability.

Similar shifts regularly occur in biotic communities in the course of their succession, or sere, from pioneer stages to climax (this does not imply that all communities inevitably arrive at their potential climax and is fairly compatible with the modern view of community systems as fluctuating mosaics of various successional stages (Hendry & McGlade 1995). For not only Abraham’s tribe, but any pioneer population tends to produce larger  $D_r$ . As a consequence, their dead mass ( $M$ ) accumulation is large relative to their comparatively small standing biomass ( $B$ ). The  $B/M$  ratio typically increases through seral stages, and this process is accompanied by a rise of taxonomic diversity. The later appearing species are, as a rule, more effective in their use of trophic resources (Bridham, Pastor, McClaugherty & Richardson 1995), which makes them less destructive than their preceding seral species and even allows them to confer a stabilising influence on their habitats.

Remarkably, the historical process of biological evolution seems to follow the same path. The early Proterozoic microbial mats have produced enormous dead mass of coaly shales (shungites) and banded iron ores constituting about 20% of the total sedimentary rock of that age (Chang, Stolz & Kirschvink 1989; James 1983). Their descendant late Proterozoic mat communities, though much more diverse (Hofmann 1976), have left a relatively small amount of organic deposits. On land, the middle Devonian coal measures have been formed by



monodominant communities of primitive algae-like vascular plants (Krassilov 1981). The arboreal tropical vegetation of the Carboniferous Period was coal-producing, while the extant tropical rain forests produce very little dead mass in comparison with their immensely large biomass.

Direct quantitative comparisons of the Carboniferous and extant vegetation in terms of biomass and productivity are hardly feasible, but some inferences can be made from the arboreal species ratios (about 50% in the former versus 70% in the latter) and the tree size (up to 40 m versus 60 m respectively). The Carboniferous plant assemblages from a single locality typically accumulating plant debris from about 1 ha of a tree stand (Krassilov 1975) are oligodominant with no more than 10 arboreal species each, while the extant rain forest stands of comparable size are mostly polydominant (occasionally monodominant in more stressful environments) (Hart, Hart & Murphy 1989) containing about 40–100 arboreal species (Wilson 1988).

These distinctions are due to the later appearing groups of organisms, such as angiosperms, being superior to their predecessors in the ability to stabilise their physical environments (e.g. soil conditions in hardwood forests in comparison with conifer forests; in particular, the tropical rain forest soils, though nutrient-poor, have fairly stable nitrogen and phosphorus concentrations) (Lewis 1986) as well as in creating more potential ecological niches for their coevolving organisms (e.g. herbivores and pollinators). In effect, evolutionary appearances of new dominant groups raise biological diversity to a higher level (in the same way the highly creative human individuals provide new social niches for other, perhaps less creative, individuals around).

Ecological succession of biotic communities thus conforms to the general trends of their historical evolution — a succession of climaxes, or clisere (Krassilov 1975), in much the same way as, according to the 'biogenetic rule', ontogenesis is a brief reiteration of phylogenesis. While the biogenetic rule relates morphological evolution to individual development, the 'ecoenogenetic rule' of the clisere — sere parallelism bridges the gap between the evolutionary and ecological time-scales thereby allowing reciprocal inferences.

The ontogenetic — phylogenetic and cenogenetic — ecogenetic parallelisms are hardly accidental. They appear to be due to directional processes sustained by telic systems, such as genome, population, ecosystem, etc., striving at definable goals, such as viable organism, continuous reproduction, effective living matter — non-living matter turnover, etc.

Insofar as the ecosystem is a living biomass producing machine (see Galley 1993 for alternative definitions) the B/M ratio is a major criterion of its effectiveness. In the progressively evolving ecosystem, B, the positive result

of its activity, would increase with structural complexity (of the canopy levels, synusia, consortial assemblages, etc.), while M, the negative result, would decrease with building up trophical pyramids. As is evident from the foregoing discussion, this is what actually happens in the course of the large time scale biosphere evolution. Both processes would create potential ecological niches as a prepattern of taxonomic diversity.

There is no *a priori* reason why the entire ecological space might not be occupied by a single generalist species (which is what the human species is striving at at the moment). However, since tolerance depends on trophic conditions (Odum 1971), it would inevitably decrease with exhaustion of trophic resources impelling this species to abandon marginal environments (as humans have to abandon costly space projects), thus leaving space for other species. Each species entry opens potential niches at the higher and lower trophic levels, thus promoting more species entries. Such positive feedback enhancing would provide for exponential rise of biological diversity. Actually the species introduction curves could be exponential in their proximal segments alone showing gradual saturation at the widely discrepant levels (May 1978), which seem to be controlled primarily by residual niche overlap and sustainable population densities:

$$Sf \sim TR/NOm + Dsm$$

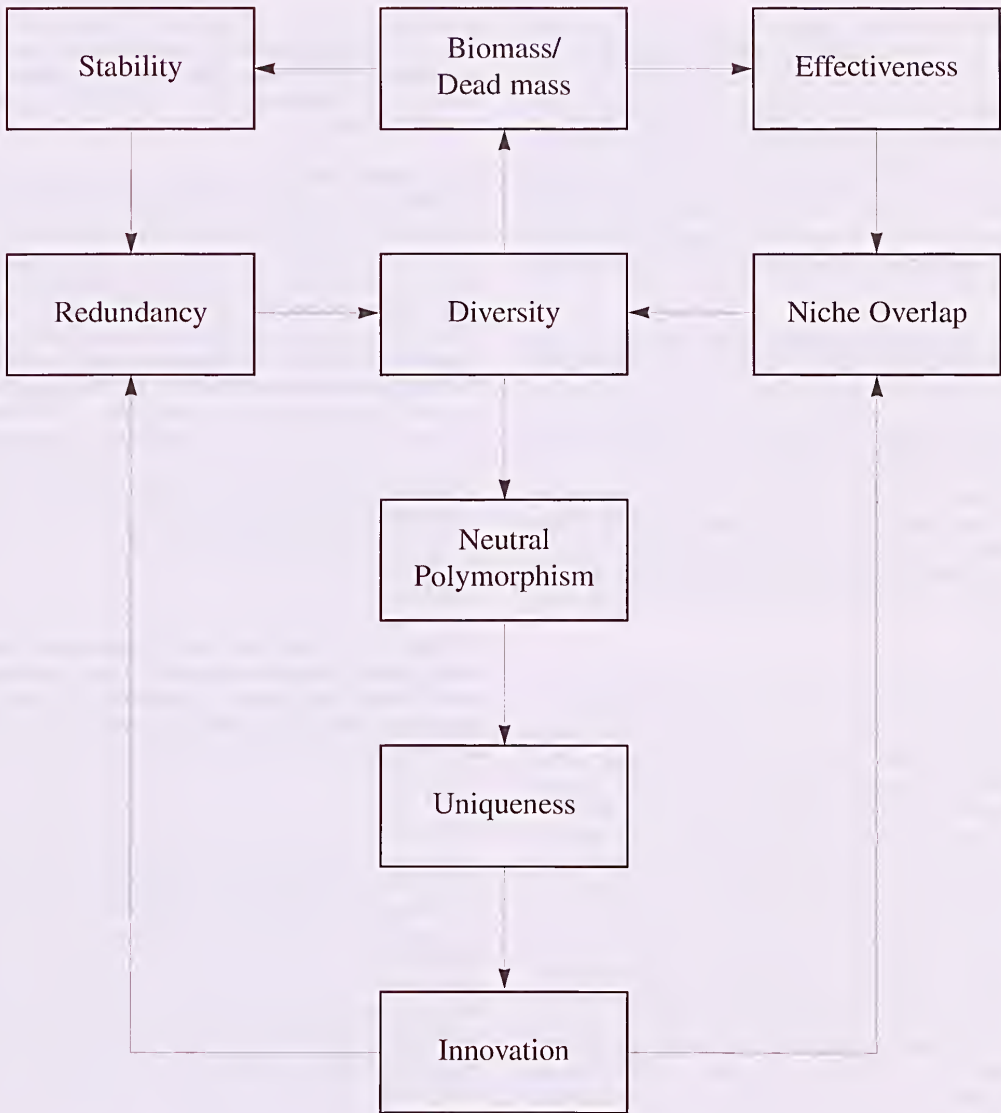
where Sf is a finite diversity of species, TR, the available trophic resources, NOm, the average niche overlap and Dsm, the average sustainable density.

Inasmuch as ecosystem evolutionary goals (above) impel a rise of Sf, there should be a reduction of NOm, Dsm, or both. Consequently, the constituent populations evolve towards a coarse-grained ecological strategy (Levins 1968) and minimal redundancy. Since the density fluctuations, the negative environmental feedback and the dead mass production relative to standing biomass tend to decrease in the process, we can identify this process as adaptation.

With NOm reduced, there would be less competition, while species entries would be due primarily to evolutionary innovations, allowing the occupation of a new niche — rather than competitive superiority. Similarly, some people assess themselves as successful competitors within the existing social structure, others as innovators in the intellectual or economic spheres creating new social niches, thereby reducing the number of redundant people. It is due to creative, rather than competitive, species and people that progress occurs in both biological and social systems.

Population redundancy in turn depends on environmental constancy: the more stable environments, the less a need in the Dr buffering and *vice versa* (thus Romans had encouraged the prolific reproduction of redundant





**Figure 1** Suggested relationships between vital parameters in the course of ecosystem evolution (explanation in the text)

citizens called proletarians and all the later appearing militant states followed their example). The diversity — redundancy — environmental stability circuit provides a long-sought explanation of the positive correlation between stability and diversity (fig. 1). A destabilising factor would impel an increase of Dr, consequently decreasing of Sf and B. Ecosystem evolution, thus, can be reversed, which actually happens under geological, climatic or human impacts. If plants increase their seed production after being eaten (see above), this does not mean that herbivory benefits them (see Liebold 1989 on the effect of predation on productivity). They, rather, have to buffer their population from total destruction by a Dr, which actually decreases their fitness. Similarly, a Dr

increase in pests is a typical reaction to pesticide impact, which is devastating not only because of its direct effect on the pest populations but also due to the indirect destructive impact of Dr. In much the same way organic pollutants instigate a redundant productivity in aquatic organisms followed by a fall of diversity in hypertrophic reservoirs (Rapport, Regier & Hutchinson 1985). In both agriculture and conservation it seems impractical to simultaneously increase productivity and diversity if these parameters are negatively correlated.

The geological record of ecosystem evolution is punctuated by the falls of diversity, which are known as mass extinctions and are correlated with major tectonic,

eustatic and climatic events (Newell 1963; Erwin 1990; Retallack 1995; Stanley & Yang 1994; Wethey 1985). Mass extinctions are especially prominent in the dominant plant and animal groups of their time. Since these groups are widespread and, by inference, tolerant to a broad range of environmental conditions, their extinction could hardly have been caused by a direct action of cooling, drought or other environmental hazards. Rather they might be endangered just by their dominant status, i.e., by being confined to the later seral stages.

In heavily impacted environments, when disturbances occur at shorter intervals than is needed to restore the climax (Tanner & Hughes 1994), ecological successions never succeed to their potential later stages, thus cutting off their climax dominants. For example, at the Cretaceous/Tertiary boundary marked by a global regression, increased volcanism and cooling, the hitherto prevailing *Sequoia* and *Parataxodium* redwoods became extinct or semi-extinct, while their understory or gap-filling broad-leaved *Corylites*, *Tiliaephyllum*, *Ushia*, etc., formed the progenitorial Arcto-Tertiary forests (Krassilov 1994).

Typically the diversity response to environmental impacts can be divided into three stages. At the first stage, *Sf* would increase due to the rise of indigenous as well as invading pioneer species (this is why 'intermediate disturbance' appears beneficial for biological diversity) (Huston 1994). In the second stage, a tail of the climax rare species would be shed. Finally a truncation of ecological successions (particularly, under destruction or fragmentation of habitats) (Tilman, May, Lehman & Nowak 1994), would result in decline and fall of the climax dominants. The surviving pioneer and early successional species would practice a high redundancy strategy stimulating high reproductive rates, in turn impelling acceleration, abbreviation and/or condensation of individual development (of which a precocious sexuality is a familiar example, the evolutionary importance of which is evident in various groups of both vertebrates and invertebrates (Bemis, 1984; McNamara 1983)) or overlap of developmental stages. Major evolutionary novelties (e.g. new plant organs formed by fusion of separate ancestral organs) (Krassilov 1991) allegedly derive from such heterochronous developments (Gould 1977; Patel 1994; Muller & Wagner 1991).

Since in the pioneer stage of ecological expansion a gene pool enrichment by hybridisation or non-sexual transduction of genetic material is potentially advantageous, there is no incentive for genetic insulation. There might be a tendency for species fusion by reciprocal genetic introgression. Species tend to be highly polymorphic and adaptively fine-grained. Contrary to the assumptions based on the fundamental theorem of natural selection (Edwards 1995), such species usually show the lowest, rather than the highest, evolutionary rates. Subsequently, while adopting a coarse-grained

strategy, they split into narrower species which are better protected from alien genetic material. A super species configuration of closely related but reproductively isolated species might arise from such speciation cycles (Krassilov 1989).

Concomitant with a switch to coarse-grained environmental strategy, a part of adaptive polymorphisms might turn non-adaptive by the narrowing of ecological niches and the loss of function. Actually, in the narrowly adapted stenobionts genetic variation appears selectively neutral at most of the polymorphic loci (Schopf & Gooch 1972). This may be accompanied by a loss of phenotypic plasticity, which correlates with moderately stressed and fluctuating environments (Kirzhner, Karol & Ronin 1995; Parsons 1991; Scheiner & Goodnight 1984; West-Eberhard 1989). Neutral polymorphism is potentially useful in acquiring new functions, e.g. marking off rare genotypes in the density-dependant mate choice. Human personality is based primarily on neutral variation of physiological and intellectual characters.

## Conclusion

In conclusion, an evolutionary model has been developed in this paper in which the ecosystem is defined as a living entity from non-living sources, the effectiveness of which can be assessed by living biomass to dead mass ratio. In the progressive evolution of an ecosystem as well as in its brief recapitulation by ecological succession, this ratio is increased (the genetic and intellectual immortality arise as a by-product) due to and concomitant with advancing structural complexity. To comply with this process, the newly added species have to be innovative — capable of opening new ecological niches — rather than competitive — capable of excluding other species. Ecosystem evolution thus promotes progressive organismic (morphological, physiological, intellectual, etc.) development. As a positive feedback, innovative species entries facilitate more species entries, thus making the increase of diversity self-sustainable. The level at which this process is slowed down depends on adaptedness — the sustainable use of environmental resources with minimal overlap of the other species' ecological niches, hence non-competitive coexistence — and a related parameter of fitness — an ability to maintain population at a low redundancy level. The latter depends on ecosystem stability buffering a sustainable density from environmental hazards.

Diversity is thus linked to stability through redundancy, a key parameter, the increase of which would reverse the ecosystem and, consequentially, organismic evolution inducing a truncation of seral and trophic chains, the corresponding decrease of biological diversity, primarily at the expense of top species, as well as developmental acceleration. Such turning points are amply documented in the fossil record and are invariably correlated with global environmental changes.



Human evolution complies to this model. Present day humans are inheritors of the early humans pioneer strategy of ecological expansion, unrestrained population growth, devastating use of trophic resources and the concomitant tense intraspecies competition. Incessant hostilities have encouraged proletarian demographic strategy. Even great empires might fall because of the ever-increasing masses of redundant people. There are, however, multiple signs of a turning point toward sustainability as a conscious goal of development including family planning, the conservationist and the animal rights movements — an incipient non-speciistic biospheric ethics. The individual priorities are gradually shifting from competitiveness to innovation. Technological developments have rendered adaptive variation, e.g. in the running speed or even in the memory capacities, non-adaptive.

The anti-Darwinian trend from useful to useless is manifested in both the biological and cultural evolution. The present day human individual variation is, for the most part, neutral (a comparison of prehistoric Venuses with modern beauties would readily show that our aesthetic ideals are shifting from the functional to the functionally neutral, and this process is faithfully reflected by the art evolution) and, with progress, more of it will turn from bearing on competitive interaction to facilitating noncompetitive coexistence of diverse individuals defining their unique sociocultural niches.

## References

- Ager, D. 1991, *New Scientist*, 128, pp. 56–57.  
 Belsky, A. J. 1986, *Am. Nat.*, 127, pp. 870–892.  
 Bemis, W. W. 1984, *Paleobiology*, 10, pp. 293–307.  
 Bridham, S. D., Paster, J., McClougherty, C. A. & Richardson, C. J. 1995, *Am. Nat.*, 145, pp. 1–21.  
 Chang, S. B. R., Stolz, J. F. & Kirschvink, J. L. 1989, *Precambrian Res.*, 43, pp. 305–317.  
 Edwards, A. W. F. 1995, *Biol. Rev.*, 69, pp. 443–474.  
 Erwin, D. H. 1990, *Ann. Rev. Ecol. Syst.*, 21, pp. 69–91.  
 Galley, F. B. 1993, *A History of the Ecosystem Concept in Ecology*. Yale University Press.  
 Gould, S. J. 1977, *Ontogeny and Phylogeny*, Harvard University Press, Cambridge, Mass.  
 Hart, T. B., Hart, J. A. & Murphy, P. G. 1989, *Am. Nat.*, 133, pp. 623–633.  
 Hendry, R. J. & McGlade, J. M. 1995, *Proc. R. Soc. Lond. B*, 259, pp. 253–259.  
 Hofmann, H. J. 1976, *J. Paleont.*, 50, pp. 1040–1073.  
 Huston, M. A. 1994, *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, UK.  
 James, H. L. 1983, *Iron Formation: Fact and Problem*. Elsevier.  
 Kirzhner, V. M., Karol, A. B. & Ronin, Y. T. 1995, *J. evol. Biol.*, 8, pp. 93–120.  
 Krassilov, V. A. 1981, *Lethaia*, 14, pp. 235–250.  
 Krassilov, V. A. 1975, *Paleoecology of Terrestrial Plants*, Wiley.  
 Krassilov, V. A. 1994, in *Cenozoic Plants and Climates of the Arctic*, eds M. C. Boulter & H. C. Fisher, Springer, pp. 115–125.  
 Krassilov, V. A. 1991, *Trends Ecol. Evol.*, 6, pp. 215–220.  
 Krassilov, V. A. 1989, *Evol. Theory*, 9, pp. 37–44.  
 Levins, R. 1968, *Evolution in Changing Environments; some theoretical explorations*, Princeton University Press, Princeton.  
 Lewis, W. M. 1986, *Ecology*, 67, pp. 1275–1282.  
 Licbold, M. A. 1989, *Am. Nat.*, 134, pp. 922–949.  
 McNamara, K. J. 1983, *J. Paleont.*, 57, pp. 461–473.  
 McNaughton, S. J. 1986, *Am. Nat.*, 128, pp. 765–770.

- Mangel, M. & Clark, C. V. 1988, *Dynamic Modelling in Behavioural Biology*, Princeton University Press, Princeton.  
 May, R. M. 1978, *Scient. Am.*, 239, pp. 160–175.  
 Muller, G. B. & Wagner, G. P. 1991, *Ann. Rev. Ecol. Syst.*, 22, pp. 229–256.  
 Newell, N. D. 1963, *Scient. Am.*, 208, pp. 76–92.  
 Odum, E. P. 1971, *Fundamentals of Ecology*, Saunders, Philadelphia.  
 Parsons, P. A. 1991, *Ann. Rev. Ecol. Syst.*, 22, pp. 1–18.  
 Patel, N. H. 1994, *Science*, 266, pp. 581–590.  
 Rapport, D. J., Regier, H. A. & Hutchinson, T. C. 1985, *Am. Nat.*, 125, pp. 617–640.  
 Retallack, G. J. 1995, *Science*, 267, pp. 77–80.  
 Stanley, S. M. & Yang, X. 1994, *Science*, 266, pp. 1340–1344.  
 Scheiner, S. M. & Goodnight, C. J. 1984, *Evolution*, 38, pp. 845–855.  
 Schopf, T. J. & Gooch, J. L. 1972, *J. Geol.*, 80, pp. 481–483.  
 Tanner, J. E. & Hughes, T. P. 1994, *Ecology*, 75, pp. 2204–2219.  
 Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994, *Nature*, 371, pp. 65–66.  
 West-Eberhard, M. J. 1989, *Ann. Rev. Ecol. Syst.*, 20, pp. 249–278.  
 Wethy, D. S. 1985, *Ecology*, 66, pp. 445–456.  
 Wilson, E. O. 1988, in *Biodiversity*, ed. E. O. Wilson, Nat. Acad. Press, pp. 3–18.





# Evolution of Biochores in the Phanerozoic

4







## 4.1 Some Aspects of Global Paleobiogeography in the Phanerozoic

Tatyana A. Grunt and Alexei Yu. Rozanov

### Abstract

Some aspects of the principles and methods of biogeographic differentiation and the allocation of biogeographical divisions of various taxonomic rank are discussed. The evolutionary pattern of marine biochoria during the Paleozoic and the Triassic period is elaborated.

Paleobiogeography is a rather broad field of knowledge, therefore, a preliminary definition of the purposes of this particular work is necessary.

Biogeographic investigations could be conducted, for example, with the purpose of the determination of chorological structure and placement of the biochoria in various taxonomic rankings, the establishing of centres of origin of different taxonomic groups, centres of diversification and the pathways, as well as the limits of using different regional zonal stratigraphic scales. Historical biogeography could consider the problems of biochoria origins and the development of different types of biotas in different basins in time (in other words it could determine some problems in the genesis of different faunistic and floristic assemblages). It is necessary to distinguish the biogeographical divisions of the shelves and epicontinental basins, littoral, sublittoral, pelagic and abyssal zones.

The diversity of the problems of this kind of research makes necessary standardisation of principles and determination of indicators for the process of establishing biogeographical divisions of different taxonomic rank. Attempts to enter such uniform principles in biogeographical divisions have been undertaken rather frequently. From this it is apparent, that biogeographical (faunistic) differentiation of the shelves and epicontinental basins is connected primarily with climatic zonation.

Although during periods of 'warm biospheres' the climatic zonation is not very clear, in the majority of cases the presence of any kind of climatic zone is rather confidently determined by the geographical distribution of some groups of marine organisms, as well as specific facies.

The concept of the latitude-climatic zonation in the hierarchy of faunistic divisions corresponds, probably, with the term super-region (realm). The divisions of this rank are also designated frequently by the freely used term - super-region.

In the structure of super-regions (realms) following standard descending hierarchy of faunistic biogeographic sub-divisions is usual: region, province, zone.

The region could be determined as a large area of water within a uniform climatic zone (super-region), never crossing the boundaries of climatic zones and being separated from the other areas of water by various isolating factors. Such isofactors, which could prevent different biotas mixing, include the absence of common shelves and being separated by the extensive deep-water spaces. It is possible to propose that the important criterion of biogeographical divisions of different rank can serve as indicators of stability in the development of large regions during significant temporary intervals within the limits of the same climatic zone. Such territories can be characterised by a reasonably long independent development of their biota as a whole with its own internal connections as well as separate elements forming the whole biota.

In the investigations of the historical biogeography of athyridids, a small group of articulate brachiopods by Grunt (1989), for example, it was established, that in different regions the representatives of this group were not only distinguishable amongst themselves on a systematic basis, but also were characterised by a reasonably long inherited development of separate taxa of high systematic level. Importantly, even on any boundary on which the systematic composition of the group occurred, the constant morphologo-ecological type of the shell (i.e. its 'vital form') usually remained invariable.

One of the best examples of such development is found in the North American biogeographical region. The platform type basins demonstrate a stable development inside the tropical climatic zone from the beginning of the Cambrian up to the middle of the Permian.

In practice, the biogeographical differentiation of modern basins into the divisions of region-rank usually represent shelves of one of the coasts of a large continent or several microcontinents, possessing common shelves and being located within a single latitude-climatic zone. However, one must remember, that today's high position of continents and the availability of narrow continental zones of shelves are abnormal. The more usual situation is the wide development of epicontinental basins.

The allocation of provinces in a structure of the regions is not connected precisely to the climatic differentiation. The latter could be determined by different methods

(arealo-genetic, taxonomic, by the introduction of different coefficients of similarity and distinction and so on). In modern marine biogeography the divisions of province rank coincide frequently with the centres of diversification. It seems that the province is usually limited to the one basin.

The transition to the areas assumes allocation biochoria, which would largely correspond with facies on a geographical sense. In any measure they, probably, answer to the facies in a geological sense. Concerning our representations, the concept of biofacies answers to the division of this rank most completely.

The elaboration of the chorological structure for particular time intervals requires the development of 'faunistic indexes'. Under the 'faunistic indexes' we bear in mind some faunistic groups, which demonstrate the main 'face' of the fauna. It could include the taxa of quite different systematic groups of quite different taxonomic rank. The sum, forming the 'faunistic index', probably should include the most prominent elements connected with earlier and later faunas.

For example, it is possible to mention the Oleneloid (Atlantic) or Redlichid (Pacific) provinces of the Early Cambrian. Boucot (1975) uses the similar concept of communities for the biogeographical characterisation of the Late Ordovician–Devonian basins.

Indexes of the same kind were used by Rozman (1977) in the process of differentiating the Ordovician basins. Thus, the England–Wales province of the Early Cambrian in the European super-region was characterised in her opinion by the Dalmanellid–Sovicbellid–Strophomenid community; the Mediterranean province by the Plectambonitid–Dalmanellid one, and the Baltic province by the Clitambonitid–Strophomenid–Orthid community. The Kazakhstan–Appalachian super-region corresponds to the Plectambonitid–Strophomenid–Orthoid community, while the Canadian–Siberian super-region was characterised by the Rhynchonellid–Ortoïd–Strophomenoid community.

Thus 'faunistic indexes' (or communities) can serve to characterise biogeographic (faunistic) divisions of different taxonomic rank. Perhaps these indexes could be represented on different maps, reflecting the chorological structure of different basins.

At present the majority of the researchers, engaged in biogeographic studies of paleozoic marine basins, base their investigations on the concept of continental drift and carry out biogeographic differentiation based on various palinspastic reconstructions.

The idea of provincial faunistic control by the geographical distance between large tectonic plates was stated about twenty years ago by Burrett (1973). By the mutual arrangement of Ordovician continental blocks and

their relative displacement, the author determined faunistic migrational potentialities. At that time this idea did not receive wide support; but, now the majority of the investigations of biogeographic differentiation is conducted with the use of various mobilistic reconstructions. At the same time, it is necessary to keep in mind that paleontological data are in essence a unique, reliable means of control of such reconstructions.

It seems important to trace the history of large basins through extended enough temporary intervals. Such attempts in recent years have been undertaken for different basins. Boucot, in his well known work of 1975, considered the evolution of a number of zoochoria during the Silurian and Devonian periods, based on the degree of similarity of a systematic composition of their populations. With this aim, quantitative valuations have been widely used. Talent (1984) examined historical biogeography of marine and terrestrial biochoria of the Australian Platform from the Cambrian up to the present. This approach seems extremely productive as a methodical plan; Talent in essence, for the first time for a large enough area, demonstrated the continuity of biogeographical divisions and the consistent replacement of marine and terrestrial biochoria through time.

Ustrizki (1993) described the main features of the Boreal basins' development during the middle and late Paleozoic. He also demonstrated the direct connections between biogeographical features and the general drift of continental blocks to the north.

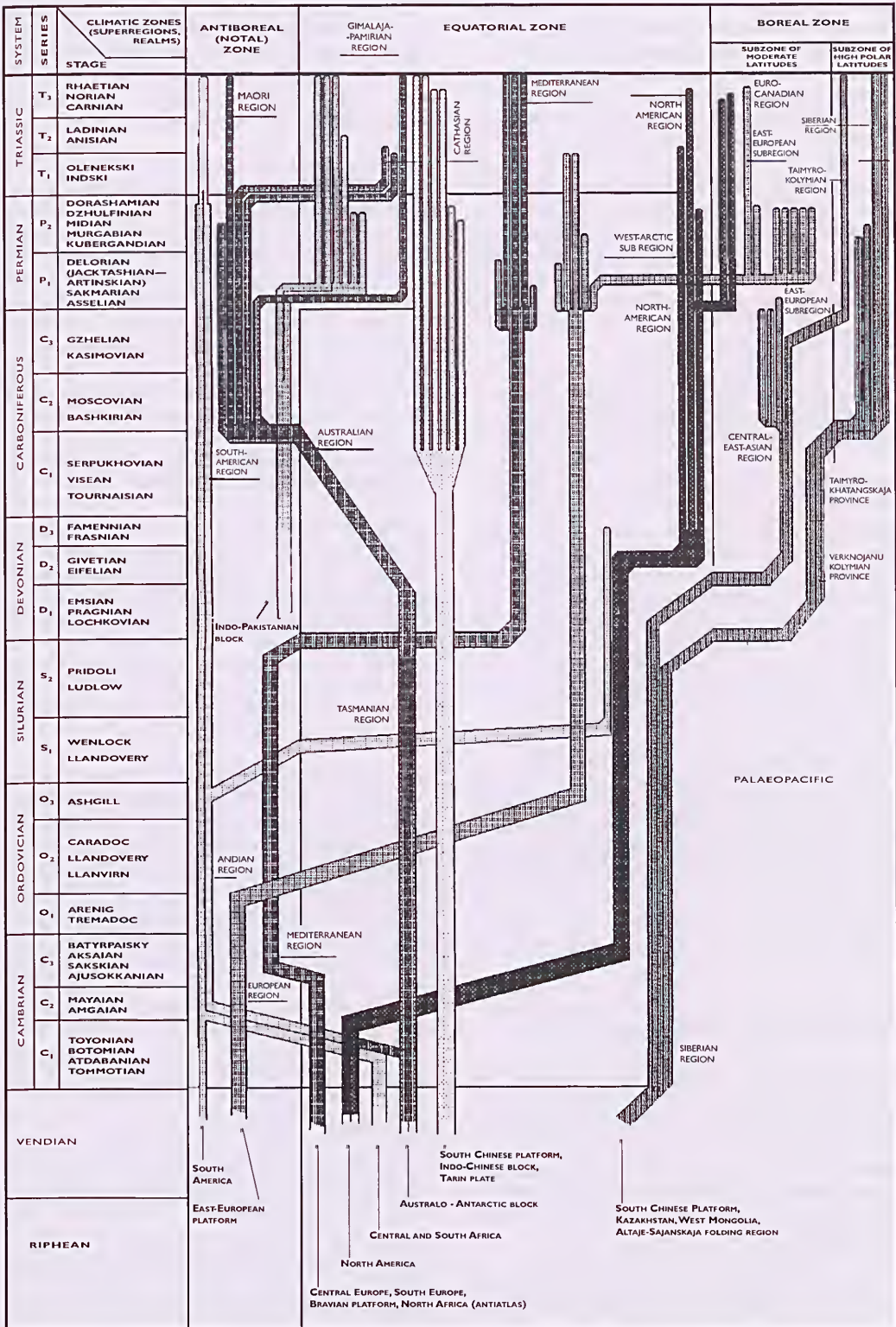
Scotese and McKerrrow (Scotese & McKerrrow 1990; Scotese 1994) in their work, containing a series of base Paleozoic palinspastic schemes, separated eight large regions. These are: North America; Siberia together with Kazakhstan; Northern Europe; Central and Southern Europe; Western Gondwana; East Gondwana; Southern China; Northern China. According to the opinion of these authors these regions were entire during the whole Paleozoic. Their location within climatic zones from the Early Cambrian up to the Late Permian was analysed. On the scheme elaborated by Scotese and McKerrrow the placement of continental blocks is shown inside equatorial or non-equatorial zones only. Thus it remains unclear, whether inside the Boreal or Notal climatic zones, any region was situated in every particular moment of geological history.

A significant amount of investigation in this area was the publication of Mejen (1986); in this the florogenetic pattern, reflecting the development of the most important branches of plants through the whole geological history of terrestrial floras is considered.

Grunt, Rozanov, Alekseeva and Manankov (1994) outlined a pattern of evolution of Paleozoic and Triassic marine biochoria. Using different climatic data, such as specific facies, the distribution of reef-building organisms and some groups of marine invertebrates, as well as



EVOLUTION OF PALEOZOIC AND TRIASSIC BIOCHORIA





paleomagnetic data, the placement of large plates and continental blocks (and their shelves) was defined inside different climatic zones (or super-regions). Using different paleontological methods the control on the provincial faunas was determined. It depends directly on geographical distance between large tectonic blocks or plates. In other words, the common shelves determined the common features between separate kratons.

One should note, that when the history of reasonably large plates of platform type are being analysed, it can be traced confidently enough. At the same time, significant difficulties can be encountered when data on active tectonic zones are being considered. The zones differ because of their complex geological history. In particular these concerns relate to the Uralian, Tian-Shanian, Pamirian, Salairian regions and so on.

In this publication we present a detailed model of the historical development of the main marine biochoria in the Paleozoic and Triassic (fig. 1).

The analysis of published materials permits us to suggest, that in the Notal (Antiboreal) zone on the Vendian–Early Cambrian boundary two large regions existed. These were: South American (I) and East European platform with its complex frame (II). The East European platform contained: the Vaigatch–North–Uralian region; the southern part of the Novaja Zemlia, Scandinavia, (except for Western Norway), Svalbard, East Newfoundland, Scotland, as well as a part of the British islands. (The numbers, specified in the text relate to the numbers specified in figure 1.)

Located in the equatorial zone there were: the block of Middle and Southern Europe (III); the North American platform and Canadian–Greenland block (IV); a block of Central and Southern Africa (V); Australo–Antarctic block (VII); Chinese platform, including its northern and southern segments; Indo–Chinese block, as well as the Tarim plate (VII); Siberian platform (s.l., including separate blocks of the north-east parts (Omolonian and Ochotsk massives), West Mongolia and Altai–Sajan areas (XI).

During the Early Paleozoic the position of the Indo–Pakistanian block (VI) is more uncertain.

The analysis of the proposed pattern allows the identification of some of the most essential features in the development of Paleozoic and Triassic biochoria. The active disintegration of the Paleopangea (Pangea-I or ‘Rodenia’) after extended rifting at about the Vendian–Cambrian boundary and movement of blocks is noticed during the Cambrian from the beginning of the Attabanian stage.

A diverse Vendian biota is known from the East–European platform, being disposed in the Notal climatic zone. No less rich is the similar Ediacarian fauna

described from Australia, in the Tropical zone. Both are connected with a terrigenous facies. The Vendian–Ediacarian fauna is also known in a limestone sequence from the Siberian Basin. However, the Notal climatic zone, along with the Tropical zone, was rather extensive. It is possible also to mark the absence of continuity between the Vendian and Cambrian biotas.

At the beginning of the Cambrian Period a large part of the platforms and continental blocks were disposed inside the Equatorial climatic zone. Then, during the Cambrian Period the blocks of Southern America, Central and Southern Africa as well as the Antarctic were moved into the Notal zone. The Australian platform remained within the tropical climatic zone. On the Cambrian–Ordovician boundary the independent supercontinent of Gondwana separated from the Paleopangea, the latter being situated inside the Notal climatic zone during practically the whole Paleozoic. Subsequently, during the whole Paleozoic the general tendency of platforms and continental blocks moving to the north is observed. The moment of crossing by separate plates or blocks through the equatorial zone can be fixed (Ustrizki 1993).

The centre of origin of many groups of skeletal invertebrates (such as archeocyathids, brachiopods, trilobites, a number of groups of molluscs) on the Siberian platform was connected to the beginning of the Early Cambrian. Distinctive migrational ways for archeocyathids are also traced, in particular. Recurring formation of a supercontinent Pangea (Pangea II) can be fixed to the middle of the Late Carboniferous, the latter existing during Permian and Triassic periods, changing its configuration only slightly.

Prior to the beginning of the Devonian Period only Notal (Antiboreal) and Equatorial (Tropical) zones are defined. In place of the Boreal zone the ocean of the Protopacific was located. From the beginning of the Devonian Period there occurred a zone of moderate latitudes in the east part of the northern hemisphere (Taimyro–Kolymian basins). Formation of the high latitudes basins inside the Arctic subzone in the eastern part of the northern hemisphere began in the Early Carboniferous (in the Post-Turnesian time). Durante (1994), identified on the Early–Middle Carboniferous boundary of this territory, postlepidofitic flora of tundra-type. During the Carboniferous the distinct zone of moderate latitudes was organised. The territories of the Central and North-East Asia, Kuznetsk Basin, Rudny Altai, Dzungarian–Balkhash and Mongolian–Ochotsk basins belonged.

The formation of a subzone of moderate latitudes of the western part of the northern hemisphere took place rather quickly in post-Sakmarian time, when the basins of the Russian platform, and Urals appeared isolated from the Palcotethys. Approximately at this time in the moderate latitudes of the western hemisphere the Canadian–Greenlandian basins appeared. Hence, during the Permian period while in the western part of the

northern hemisphere the basins of moderate latitudes were present, there was a zone of high arctic latitudes in the eastern hemisphere. The zone of moderate latitudes was not expressed here at that time. In other words, during the Permian in the eastern hemisphere the basins of the moderate subzone of the Boreal climatic zone, and the western hemisphere the basins of high pole latitudes are absent.

The basins of moderate latitudes of the western hemisphere were historically connected with the Tethyan basins, at the same time as the basins of high pole latitudes of the eastern hemisphere had much in common with the frame of the Siberian platforms. In fact, these two large regions were developed independently. Biogeographical communications between them were actively displayed only during the Kungurian-Ufimian time during maximum marine transgressions. It is, thus, not surprising that stratigraphic correlations between these two regions are extremely hindered.

During the Viscan the Australian platform passed from the Tropical zone into the Notal zone. Thus, the special separation of the Australian and Taimyro-Kolymian basins took place at that time. Since then they have lain symmetrically about the equator in the northern and southern hemispheres. At the same time, these two systems had a rather long common previous history, through their location in the Equatorial zone. Probably, from this point of view the phenomenon of bi-polar distribution in the development of some groups of articulate brachiopods (such as ingellaroid spiriferids or spine-bearing productids as well as *Inoceramus*-like bivalves) can be explained.

Detailing the pattern, it is possible to determine a history of development of the Paleotethys. It is important to note that the formation of the Paleotethys, as a uniform pool, began in the Carboniferous. Uniform biogeographical treatment only occurs in post-Sakmarian time when, in its numerous terrains and continental blocks, it formed its Perigondwanian coast. It is possible to establish the time of passage over the paleoequator by the separate blocks, and determine the northern and southern subequatorial zones.

## Conclusions

The general tendency in the development of biochoria during the Paleozoic is the growing differentiation in time. On this common background the cyclic shift of cosmopolitan periods (Early Silurian, Late Devonian, Early Carboniferous, Early Triassic) and high levels of provincialism (Late Cambrian, Early Ordovician, Early Devonian, Permian) can be seen.

However, a significant reduction in the degree of endemism of the basins and a general reduction of diversity during the Triassic is apparent. It seems, that the basins of an equatorial zone during the Paleozoic could

play a primary role in the diversification processes. As a centre of origin of many groups of marine 'skeletal' invertebrates in the Paleozoic the Early Cambrian basins of the Siberian platform, being situated at this time in the equatorial zone could be considered. The end of the Permian period saw practically the complete extinction of the Paleozoic marine biota. The maximum of diversity of marine invertebrates was found at that time in the Paleotethys. This basin during Early and Middle Triassic has been, in essence, the centre of the origin and formation of new Mesozoic marine biota. However, the occurrence and further development of a number of marine invertebrate groups could be connected to some other climatic zones.

## References

- Alekseeva, R. E. 1992, 'Paleozoogeography of the Eurasia in early Devonian', *Palaeontological Journal*, no. 1, pp. 3–13.
- Boucot, A. J. 1975, *Evolution and Extinction Rate Controls. Developments in Palaeontology and Stratigraphy*, 1, New York, 427 pp.
- Burrett, C. 1973, 'Ordovician biogeography and continental drift', *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 13 no. 3, pp. 161–201.
- Dagis, A. 1974, *Triassic brachiopods (morphology, phylogeny, stratigraphical significance and biogeography)*, Nauka, Novosibirsk.
- Debrenne, F., Zhuravlev, A. Yu., Rozanov, A. Yu. 1989, 'Regular archaeocyaths', *Trans. Palaeontological Inst. of the A.S. USSR*.
- Debrenne, F., Zhuravlev, A. Yu., Rozanov, A. 1990, 'Regular Archaeocyaths', *Cahiers de paléontologie Editions du Centre National de las Recherche Scientifique, Paris*.
- Durante, M. V. 1994, 'Late Palaeozoic floras of Angarida', *Écosystème reorganization and evolution of the biosphere*, vol. 1, Nedra, Moscow, pp. 248–258.
- Grunt, T. A. 1989, 'Biogeography of the brachiopods of the order Athyridida', *Palaeontological Journ.*, no. 2, pp. 40–51.
- Grunt, T. A., Rozanov, A. Yu., Alekseeva, R. E. & Manakov, I. N. 1994, 'Some approaches to the problems of historical biogeography of marine basins', in *Ecosystems reorganisation and evolution of biosphere*, vol. 1, Nedra, Moscow, pp. 205–212.
- Gurianova, E. F. 1957, *Regularities of distribution of recent marine fauna and principles of the subdivision of the world ocean. Problems of the palaeobiogeography and biostratigraphy*, Gosgeoltekhizdat, Moscow, pp. 15–27.
- Macridin, V. P. 1965, *Methodic of palaeobiogeographical subdivisions. Theses of reports on the 11th session of VPO*, Nedra, Leningrad, pp. 24–25.
- Mejen, S. V. 1986, 'Florogenesis and evolution of plants', *Priroda*, no. 11, pp. 47–57.
- Nesis, K. N. 1982, *Zoogeography of the world ocean*, Nauka, Moscow, pp. 114–134.
- Rozanov, A. Yu. 1984, *Some aspects of study of bio and palaeogeography of Early Cambrian investigations*, 27th International Geological Congress, Palaeontology, Section C. 02, Nauka, Moscow, The reports Vol. 2, pp. 84–93.
- Rozman, K. S. 1977, 'Biostratigraphy and zoogeography of the Late Ordovician of Northern Asia and Northern America (based on Brachiopods)', *Trans. Geological Institute, A.S. USSR*, vol. 305.
- Scotese, C. R. & McKerrow, W. S. 1990, 'Revised World maps and introduction. Palaeogeography and Biogeography', *Geological Society Memoir*, no. 12, pp. 1–21.
- Shevyrev, A. A. 1990, 'Biogeography of the Triassic ammonoidea (Cephalopoda)', *Trans. of Palaeontological Institute A.S. USSR*, vol. 243, pp. 97–119.
- Talent, J. A. 1984, 'Australian biogeography past and present: determinations and implications', in *Phanerozoic earth history of Australia*, ed. J. J. Veevers, Clarendon Press, Oxford, pp. 58–93.
- Ustrizki, V. I. 1993, 'Biogeography of the boreal area in palaeozoic stratigraphy', *Geological Correlation*, vol. 1 no. 2, pp. 67–77.
- Yuferev, O. V. 1973, 'Carboniferous of the Siberian biogeographic belt', Nauka, Novosibirsk.





## 4.2 Biogeographic Zonation of the Late Eocene — Early Miocene Tethys–Paratethys Basins Based on Bivalve Data

S. V. Popov

### Abstract

Zoogeographic subdivisions of Late Eocene, Oligocene, Early Miocene shelves in Western Eurasia and North Africa are distinguished using restored generic and specific compositions of the bivalves and analysis of the areas of the most characteristic genera and species. The Neotethyan (tropical) and North-European (subtropical) regions are well for the Priabonian. The former was divided into an Indo–African and an ancient Mediterranean subregion. During Rupelian, Neotethyan faunistic composition was losing diversity, North African shelf molluscs showed similarities to South European faunas. A new West Mediterranean fauna began forming in the Chattian. After the Early Miocene warming, it has been species-rich, including the modern day fauna. During the Early Miocene these molluscs of West Mediterranean origin invaded the North Sea Basin, Central and Eastern Paratethys and Indo-Persian coast.

Paleogene biogeographical zonation, for both open ocean and continental shelf areas, can be distinguished from modern day zonation because of the existence of the Tethys Ocean and circum-global sub-Equatorial currents. In the northern hemisphere a complex system of inland and marginal seas with a belt of islands developed because of the Alpine Fold system (see fig. 2 (c)). Europe was archipelagic at that time, bounded by Neo-Tethyan seas to the south, the Atlantic, and the Norwegian–Greenland sea to the west, the West–Siberian, Turgai and Turan seas to the east.

Using collections in The Paleontological Institute and materials of R. L. Merklin, O. V. Amitrov, G. Kh. Salibaev, P. M. Aslanyan, Yu. Karaguleva, A. Rusu, J. Senes et al. I have been able to study Late Eocene, Oligocene and Early Miocene bivalves of the Eastern Paratethys (Popov et al. 1993), Central Paratethys, Southern Bulgaria and Armenia, which has made it possible to compare genera and species from these basins with published data on neighbouring paleobasins. From this database distribution patterns of shallow bivalve assemblages in the Tethys–Paratethys seas have been plotted.

Species of each assemblage were listed for each paleobasin and summary tables compiled of genera (subgenera) composition for the Priabonian, species for the Rupelian, Chattian and Early Miocene. As a taxonomic base, I used a slightly modified system of Bivalvia, published in the Treatise (1969). These lists were published partly (Popov 1994). Graphs were used to illustrate the relative abundance, thermophilic and compositional similarity of assemblages (fig. 1 (b)). The thermophilic characteristics of bivalves were estimated according to climatic zonation of genera and subgenera in present seas (Popov et al. 1993, table 5). Then I calculated the number of common species (or subgenera) for each assemblage pair as twin Preston's coefficients (Popov 1994). All this information, was used to distinguish the most significant zoogeographic boundaries, the rank of

which was estimated by comparison with the present mollusc distribution.

### Results

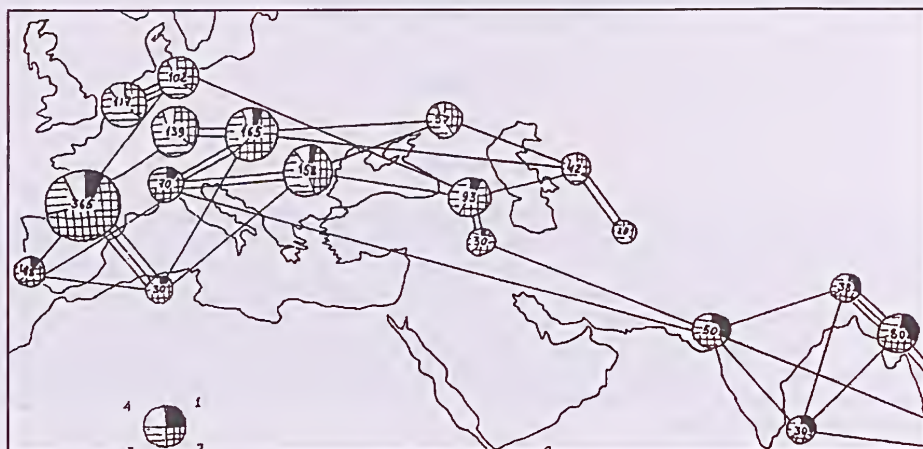
#### *Priabonian*

The results of comparing the subgeneric compositions of assemblage pairs and their thermophilic characteristics (fig. 1) demonstrates that faunas from southern and central Europe and from Transcaucasia are interrelated and distinct on the one hand from molluscs of north-west and eastern Europe, Transcaspia and on the other hand North Africa and India. If comparison of species composition were made, the difference would be greater. North African (Egypt, Upper Moccattam subformation — Strougo 1977) molluscan species show little in common with European assemblages. Among Western Eurasian species there were many widespread taxa, but the dissimilarity between southern and northern European faunas becomes evident when tracing distribution of discrete species and genera. The northern faunas seem less interrelated to the southern assemblages and were changing in composition during Priabonian time. Transcaspian molluscs differ as greatly from Latdorfian faunas as from the Priabonian Mandrikovkan assemblage of the Ukraine. Nearly half of the bivalve species were endemic Transcaspian forms.

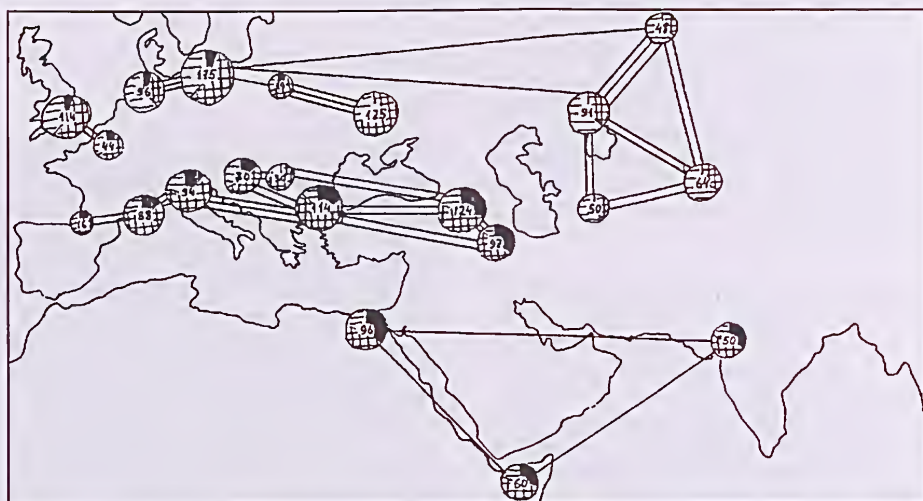
#### *Rupelian*

Global cooling at the end of Priabonian times caused a decrease in biodiversity correlated with eustatic regression. The Turgai Sea separated West Siberian and Middle Asia (see fig. 2 (b)). The Paratethys was separated from the Tethys as a result of the uplift in the Alpine fold-belt. Marine faunal realms changed greatly. Differences between bivalve associations of north-western Europe, central and southern Europe, Transcaspia, Transcaucasia ceased to exist; taxonomic composition and regional boundaries were changing. The Tethyan fauna continued

## A. Early Miocene



## B. Late Miocene



**Figure 1** Circle diagrams of abundance and climatic affinity of the Tethys-Paratethys bivalve associations. Square of the circles is proportional to the number of species, indicated in the centre. Sector squares reflect relative abundances of the following: 1 - species of tropical genera; 2 - tropical-subtropical ones; 3 - widespread occurrence; 4 - mainly boreal. Connecting lines show the degree of compositional similarity between assemblages according to the threshold values of Preston's coefficients (Popov 1994).

to exist in Transylvania, southern Bulgaria and Armenia, but its composition sharply changed in the Carpathian Basin, northern Bulgaria and on the Georgian shelf. North African molluscs lost their peculiarity and became similar to south European faunas as a result of the elevation of Asia Minor and the appearance of shallow-water connections and the closed system of ocean currents in the eastern Mediterranean. Decreased diversity of Neo-Tethyan molluscs may have resulted from southward migrations: some species, which in Priabonian times were known in northern assemblages only, invaded the Neo-Tethys in the Rupelian (e.g. *Barbatia nysti*, *Anadara sulcicosta*, *Astarte kickxi*).

### Chatian

In the Norwegian-Greenland and Paratethys basins the situation in the Chatian was similar to that of the Rupelian. The main direction of mollusc migrations remained eastward and southward from the Norwegian-Greenland Sea. The process of the faunistic integration continued: more than twenty bivalve species, earlier known in northern basins only, appeared in the Mediterranean after the Chatian (against eight since the Rupelian). There were differences in the faunas in northern basins and the Neo-Tethys, but a broad transitional zone was formed between them (the Central



Paratethys during Egerian). Many species and a few genera were limited to the northern basins. The most characteristic taxa — *Chlamys bifida* — zonal species of the Chattian A, was widespread from Germany to the Aral Sea. In the second part of Chattian endemic, euryhaline species dominated in the Eastern Paratethys assemblages (*Plagiocardium abundans*, *Cerastoderma prigorovskii*, *Corbula helmsereni*). Mediterranean mollusc data is not rich, only an Italian association is known for this area (near 100 species by Venzo 1937; Accordi 1955). It includes many new species, which became widespread in the Miocene.

### Early Miocene

Two important events determined the Early Miocene evolution of the coastal bivalve fauna of West Eurasia:

- (1) as a consequence of global warming which had commenced the primary direction of molluscan migrations during the Oligocene of north to south was reversed;
- (2) the basin of the north-western Europe lost their epicontinental connections with the other European basins.

These events caused considerable reorganization of the molluscan faunas especially in the Paratethys. These changes are seen at their greatest during Burdigalian (Eggenburgian, Hemmoorian, Sakaraulian), when the composition of the Aquitanian bivalves had transitional Oligo-Miocene character both in the North Sea basin and in the Paratethys. The transgressive character of the Burdigalian deposits, abundance of sandy facies and a diversity of warm-water assemblages supported a rather rich fauna of bivalves (fig. 1 (a)). The most distinct connections are traced among Central Paratethys assemblages and between them and bivalves of the Mediterranean part of the Tethys, which include the faunas of the Northern African and Aquitanian coasts. Among the most widespread species in the Early Miocene, there were many new Miocene ones, significant proportions of them being represented by present-living species (*Glycymeris bimaculata*, *Divalinga ornata*, *Chama gryphoides* et al.). Some species, which were found in the warmest water southern assemblages only during Chattian time, became widespread in the Miocene. Oligocene species only predominated among species common to Central Europe, the North Sea and the Eastern Paratethys, indicating difficulty of migration during the Early Miocene. The data on the Early Miocene fauna of the Eastern Paratethys are extremely scanty now. Almost nothing is known about coastal marine molluscs of the northern part of the latter basin. In the southern (Transcaucasian) part, Sakaraulian s.s. molluscs existed. They included a lot of allochthonous species (30%), which are now considered as Indo-Persian forms (Nevesskaya et al. 1991; Popov et al. 1993).

## Zoogeographic Zonation

### Priabonian

The most significant zoogeographic boundaries were between the faunas of :

- (1) the southern coastal zone of the Neo-Tethys (North Africa, North India);
- (2) the Neo-Tethys northern shelf (South Europe, Transcaucasia);
- (3) the Epicontinental basins of north-west Europe and Transcaspia.

The boundary between Neo-Tethyan and north-west European mollusc faunas coincided with northern boundary of 'Nummulitic seas' in the Priabonian time. In contrast, data on *Nummulites* shows a similarity between the taxonomic compositions of their assemblages from southern Europe, India and northern and eastern Africa (Strougo 1977). Taking this into account, I consider the North African and Indian coasts as an Indo-African subregion of the tropical Neotethyan region, where the deep areas of the Tethys and sublatitudinal currents were barriers to the migration of coastal molluscs.

Taking into account stable differences between southern and northern European molluscs and other faunal groups (since the Mesozoic), these areas may be defined as the Neo-Tethyan (tropical) and North European (subtropical) zoogeographic regions. The Neo-Tethyan region was divided into Indo-African and ancient Mediterranean subregions. The latter included the present territories of the northern Mediterranean, basins of Alps, Carpathians, southern Bulgaria (Karaguleva 1964) and Transcaucasia (fig. 2 (a)). All these faunas show a high degree of similarity and should probably be considered a single superprovince (or province).

The northern European assemblages were more differentiated. It is possible to distinguish provinces within the subregion: Anglo-Parisian (with euryhaline mollusc's composition), Latdorfian, Mandrikovian, Turan, divisible into northern (Kazakhstan) and southern (Tadzhik-Fergana) subprovinces.

### Rupelian

The African coast had lost independence and was included in the ancient Mediterranean subregion for the Rupelian, as a result of the closing of the Tethys ocean. The differences between Neo-Tethyan and North European regions stayed evident, but their boundary was moved southward: the Alpine foredeep, Carpathian basin and the northern part of Transcaucasia came into the North-European region. The Lesser Caucasus became a continental barrier between the Armenian bay of the Tethys and the Eastern Paratethys. There are three evident faunal provinces in the North-European region: Germanian (Rupelian), Central European (Merian) and Eastern Paratethyan (Pshchikhan) (fig. 2 (b)).



A. Early Miocene 20 M.A.



B. Oligocene 30 M.A.



C. Late Eocene 40 M.A.



## Chattian

Less evident, but still recognizable differences continued to exist between North-European and Mediterranean regions. The former region included Germanian and Eastern Paratethyan provinces. The central European one became a broad intermediate zone between the two regions.

Tethyan molluscs of the 'Eocene type' had become extinct and a new Mediterranean fauna, containing a present-living species began to appear.

## Early Miocene

The North-European region, which had been traced (according to publications) at least since the Cretaceous probably disappeared in the Early Miocene. Burdigalian molluscs of the whole studied area become so similar that it could be considered to be within a single Mediterranean subregion (fig. 3 (c)). The latter included:

- (1) the Hemmoorian Province occupying north-west Europe (North Sea basin);
- (2) the Eggenburgian Province occupying Prealpine and Carpathian basins;
- (3) the Burdigalian s.s. Province occupying the Neotethyan basin including the Aquitanian basin;

## Left

**Figure 2** Zoogeographic zonation of the Tethys-Paratethys shelves, based on the Priabonian (C), Oligocene (B) and Early Miocene (A) bivalve molluscs:

- I - Ancient Mediterranean region:
  - 1-Germanian (Hemmoorean) province;
  - 2-Eastern Paratethyan one;
  - 3-Central Paratethyan (Eggenburgian);
  - 4-Burdigalian province.
- II - North-European region:
  - 1-Germanian (Rupel-Chattian) province;
  - 2-Eastern Paratethyan (Psechkhian-Kalmykian) one;
  - 3-Central Paratethyan (Kiscel-Egerian) province;
  - 4-Neotethyan region.
- III - North-European region:
  - 1-Lafdorphan province;
  - 2-Mandrikovian one;
  - 3-Turan province;
  - 4-Priabonian subregion;
  - 5-Indo-African subregion;
  - 6-coastline and shelf;
  - 7-main nappes, overthrusts and fractures.

As the base of these schemes it was used unpublished palinspastic reconstructions for 20, 30, 40, M.A. from 'Paleogeographic Atlas of the Eurasia' (Plate Tectonics Institute RAS).

- (4) the Sakaraulian Province (Eastern Paratethys). Sakaraulian s.s. molluscs from Georgia included both species of Mediterranean origin (common with central European associations) and Indo-Persian forms.

The research described in this publication was prepared in accordance with the programme of investigations of the Russian national group of the Paratethys Project (N 343 IGCP) and was made possible in part by Grant N J15100 from the International Science Foundation and the Russian Government.

## References

- Accordi, B. 1955, 'Stratigrafia o paleontologia delle formazioni oligomioceniche del Trevigiano orientale', *Mem. Inst. Geol. Mineral*, 19, pp. 3-64.
- Karagyuleva, Yu. D. 1964, 'The Paleogene molluscs. Fossils of Bulgaria. Sofia', *Bull. Akad. Nauk.*, 6a, 270 pp. (in Bulgarian).
- Moore, Raymond C. (ed.) 1969, *Treatise on invertebrate paleontology Pt. N. Bivalvia*, Geol. Soc. Amer., Univ. Kansas, 952 pp.
- Nevevskaya, L. A., Gontcharova, I. A., Ilyina, L. B. et al. 1986, 'History of the Paratethys Neogene molluscs', *Nauka*, 208 pp. (in Russian).
- Popov, S. V. 1994, 'Zoogeography of the Late Eocene Basins on the Western Eurasia based on bivalve molluscs', *Strat. Geol. Correlation*, vol. 3 no. 2, pp. 83-97.
- Popov, S. V., Voronina, A. A. & Gontcharova, I. A. 1993, *Stratigraphy and bivalve molluscs of the Oligocene and Lower Miocene from Eastern Paratethys*, Nauka, Moscow, 207 pp. (in Russian).
- Strougo, A. 1977, 'Le "Biarritzien" et le Priabonien en Egypte et leurs faunes de Bivalves', *Trav. Labor. Paleontol. Orsay*, 247 pp.





### 4.3 Historical Zoogeography of Terrestrial Tetrapods and a New Method of Global Palaeogeographical Reconstructions

N. N. Kalandadze and A. S. Rautian

Editor's note: This paper has been left in its original form to allow the free philosophical approach of the authors to be preserved.

The main goals of our research on the historical zoogeography of terrestrial (non-marine and non-flying) tetrapods (Kalandadze & Rautian 1980, 1981, 1983, 1991, 1992) are:

- (1) the creation of a sequential palaeontological substantiation of zoogeographical division of Wallas, and;
- (2) the use of the intercontinental faunistic connections for global small-scale palaeogeographical reconstruction, primarily, of conjunctions and disjunctions or large territories of land at different stages of geological history of terrestrial tetrapods. This article provides brief information on the method used by us and its use in the understanding of the most important events in mammalian geological history.

#### Materials and methods

Historical zoogeography, as indicated by Wallas (1876) begins with the global faunistic subdivision. Its understanding requires the analysis of palaeontological material throughout the time of formation of the faunas.

Therefore, we utilised all of the accessible (mainly published) data about geographical and stratigraphic distribution of fossil and modern terrestrial tetrapods. The faunas were compared at the level of genera and higher. We tried to avoid subjectivity of palaeogeographical judgments, at least in the beginning of the research. Therefore, all the faunas were compared with each other, irrespective of their present or past location on the surface of the Earth.

This allowed us to develop a small-scale global palaeogeographical reconstruction based on the terrestrial tetrapod material (fig. 1). The preliminary reconstruction of faunistic connections and zoogeographical division were built for each division of the stratigraphic scale and, as far as palaeontological material permitted on a global basis.

The deficiency of palaeontological information for terrestrial tetrapods has not allowed us to create a preliminary reconstruction for the Devonian or the Early and Middle Jurassic. Our search for the causes of the exclusively poor faunas found in the Early and Middle Jurassic has lead to the discovery of the largest ecological crisis in the history of terrestrial tetrapods. A crisis that was accompanied by a sharp decrease in their taxonomic

diversity (Kalandadze & Rautian 1983, 1993a, b). Independently of us the same crisis was noted by Benton (1985, 1987).

During the Permian and Carboniferous glacial period in Gondwana (Chumakov 1984, 1993), terrestrial vertebrates are known in the Carboniferous almost exclusively from Northern America and Western Europe, and in the Early Permian to the north of the Tethys Sea. Therefore, the then global reconstructions only begin with the Late Permian.

Discarding the false (inherited from the previous epochs) faunistic connections from each of the preliminary reconstructions was achieved through a combination of two operations.

#### *Operation by 'subtraction'*

If the direct connection between two faunas is established by certain taxa that can be accounted for by known distribution in the previous periods, we withdrew such taxa from consideration of connections for the given time.

#### *Operation of 'reduction'*

If the direct connection between faunas of two regions appears to be weaker, or can be completely reduced to two (or greater number) mediating connections (i.e. each, or the overwhelming majority of the taxa with direction connection corresponded to the same taxa of the mediating connections), we considered such a connection to be a false one caused by the connection of two faunas with the help of a third, or several other faunas.

Only after the substantial reduction of the level of 'refuge of ignorance' by the creation of the estimated picture of the history of the global terrestrial faunistic division (based upon terrestrial tetrapods), did we dare to make regional and short-term (in geological time scale) analysis of the faunistic connections, which allowed us to specify a series of important details, first of all related to the age of the faunas.

The presence of valid faunistic connections in the palaeogeographical reconstruction was interpreted as evidence to overland connections between the corresponding territories for the duration of the whole or a part of the given interval of geological time; and their total absence, as the evidence to marine isolation of the corresponding territories during the whole given interval of geological time. The main goal of our work was to create a sequence of palaeogeographical reconstructions, which would permit us to describe all of the known data about



**Figure 1** Global palaeogeographical reconstructions established on the data on historical zoogeography of terrestrial tetrapods.

In the first four reconstructions, for the times from the Early Permian until the Middle Trias, similarity between the shapes of ancient and modern continents is low. Therefore, the abbreviations of modern geographical names are given, i.e. N Am - North America, S Am - South America, W Eu - continental Western Europe, S-W Eu the southern parts of Western Europe, Sc - Scotland, E Eu - Eastern Europe, As - Asia, Ind - India, Af - Africa, Au - Australia, Ant - Antarctica.

In the following reconstructions, from the Late Trias until the Recent, patterns of ancient continents become recognizable. Dotted lines show the patterns of ancient continents, for which there were not enough palaeontological data referring to the corresponding geological time to obtain sure reconstructions. In these cases the projections of reconstructions of previous and/or following times were used.

geographical and stratigraphic distribution of all the modern and fossil terrestrial tetrapods in the least contradictory manner. A script of their global faunagenesis should be free (or nearly free) of phylogenetic and phylogenetic contradictions. It is not surprising that only one palaeogeographical reconstruction (fig. 1) appeared to be in agreement with such extremely demanding zoogeographical requirements.

The few remaining contradictions are the inevitable consequence of spatial and temporal incompleteness of the fossil record, inexact determinations of a series of partial palaeontological remains and imperfection of the phylogenetic system of terrestrial vertebrates. However,

the principles of irreversibility of evolution, monophyletic, monotypic, and monochronic origin of taxa of phylogenetic systems (Skarlato & Starobogatov 1974), have allowed us to reconstruct a number of missing links by means of the following common assumptions (in the sense used by Rasnitsyn 1988):

- (1) a disjunctive distribution of a taxon is evidence for the existence of its representatives in the intermediate territory;
- (2) the presence of representatives of a taxon in isolated faunas is evidence of its existence in the epoch when the faunas of the territories were in direct or indirect contact. Such reconstructions of geographical and stratigraphical distribution of



taxa have allowed us to considerably reduce contradictions within the general script of faunagenesis. In particular they have allowed us to develop palaeogeographical reconstruction for the Early and Middle Jurassic.

### Historical zoogeography and the main events of the mammal history

Separation of the mammal-like reptile branch (Synapsida) took place no later than the Middle Carboniferous, i.e. before the separation of Europe – American and Gondwanian zoogeographical areas. Phylogenesis of remote (Therapsida) and direct ancestors of mammals (Theriodontia, Cynodontia) was connected with Gondwana. Mammals (Prototheria and Theria) had a global distribution at the very beginning of their history, in the Late Trias. At that time the greatest consolidation of all the tetrapod faunas was observed. This had never occurred either earlier (at least after the Early Permian) or later (fig. 1). Zoogeographical 'Pangea' of the Late Trias destroyed all the previous zoogeographical divisions. Therefore, the origins of the historical zoogeography of modern faunas cannot extend too far into the past, at least further than the Late Trias (Kalandadze & Rautian 1980, 1981, 1983, 1991). Obviously, the acquisition of the bases of homiothermy could be referred to that time (Rautian 1990). Mammals became the dominant small-sized class of terrestrial vertebrates in the second half of the Late Jurassic because of the largest ecological crisis in the history of terrestrial tetrapods (Kalandadze & Rautian 1993a). At the same time Multituberculata (the most ancient small-sized efficient phytophagous tetrapods) came onto the ecological scene. They laid down the prerequisites of the formation of the food pyramid in subdominant community (see Olson 1966) of small-sized tetrapods (Kalandadze & Rautian 1995).

The separation of the southern block of continents (South America–Antarctica–Australia) occurred not later than in the Middle Jurassic (fig. 1). Divergence of Prototheria into Monotremata and Multituberculata, as well as Theria (Peramuria) into Metatheria and Eutheria we suggest is connected with this event.

Asia and Europe were separated by the Turgai Sea no later than in the end of the Middle Jurassic. The origin of Cimolodonta, Caniformai, Deltatheridia and their probable derivatives Creodonta, Menotyphla (including Proteutheria), Mixodontia and relative to them Lagomorpha, and probably Taeniodonta was obviously connected with the Asian centre of mammal radiation. The origin of Plagiaulacida, Lipotyphla, Edentata (including Tubulidentata and Pholidota), the ancestors of Primates (Strepsirhini and Haplorhini) and Rodentia we suggest was connected with the Western centre (Africa–Europe–North America). The absence of Lipotyphla in the Asian centre and Menotyphla (sensu Butler) in the Western centre makes us presume that the whole diversity of placental mammals originated from the

branch of carnivorous mammals (carnivora including Aegialodontia, Deltatheridia, Creodonta), but not from Insectivora. Similarly, in parallel, a branch of the Metatheria, insectivorous groups (Peramelida, Myrmecobiidae, Notoryctidae, Caenolestidae, Necrolestidae) originated from the carnivorous branch Didelphoidea–Dasyuroidea.

At the boundary of the Jurassic and Cretaceous, Africa, Europe and North America separated. The fauna of Madagascar, isolated at least for the whole of the Cenozoic, permits us to judge the autochthonous fauna of Africa, with which the origin of Feliformia, Soricomorph, Strepsirhini, Miomorpha (Cricetidae), Tubulidentata was connected.

The Autochthonous fauna of South America lacks mammals of Asian origin. The rising of the most ancient Beringia and the beginning of intensive faunistic exchange through it goes back to the end of the Early Cretaceous (Aptian and Albian). For example, Menotyphla, the ancestors of Dermoptera (incl. Plesiodapiformes and Apatotheria), did not penetrate into South America. Therefore, the contact between North and South America should have occurred not later than in the middle of the Early Cretaceous. At that time Didelphoidea penetrated from South America into North America; and the placentals: Tarsiiformes, the ancestors of Platyrrhini, and the ancestors of Caviomorpha, Pilosa, including Myrmecophagidae, Notioprogonia, Mioclaeninae, Pantolambdinae penetrated from North America into South America. In the autochthonous fauna of South American carnivores are represented by marsupials (Borhyaenoidae and Coenolestidae), whereas phytophagans (with a few exceptions: Polydolopidae, Groeberiidae, Argiolagidae) are represented by placental mammals (Caviomorpha, Notoungulata, Astrapotheria, Pyrotheria, Didolodontidae, Litopterna). North America is the native land of ungulates (Ungulata: Notoungulata and Condylarthra) and simultaneously the only continent in which there is a lack of autochthonous carnivorous placentals. It testifies to an assumption that at the times of meeting of the marsupials and placentals in the Early Cretaceous the first of them were represented by more specialized carnivores, whereas the second owed the expressed preadaptations to phytophagy. It is rather probable that Didelphoidea stimulated the specialization of the ancestors of the ungulates under those conditions. Thus, the carnivorous specialization of Condylarthra was, evidently, secondary. The absence of a Beringian connection from the end of the Cretaceous up to the middle of the Paleocene in combination with the origin of Artiodactyla in North America and of Cetacea on the coasts of the Tethys in those times, allowed us to suppose that the age of their common ancestors, carnivorous Condylarthra, was the Late Cretaceous.

The absence of Diprotodonta in America and the placentals in the pre-Miocene faunas of Australia testifies to isolation of the latter till the middle of the Early



Cretaceous. The findings of South American groups (Polydolopidae, Tardigrada, Astrapotheria, Litopterna, Phorusrhacidae, Sebecidae) in Antarctica (Hooker 1992) testifies to connection of the two after the separation of Australia.

## References

- Benton, M. 1985, 'Mass extinction among families of non-marine tetrapods', *Nature*, vol. 306 no. 6031, pp. 811–814.
- Benton, M. 1987, 'Mass extinction among families of non-marine tetrapods: the data', *Mém. Soc. Geol. (France)*, no. 150, pp. 21–32.
- Chumakov, N. M. 1984, 'The main glacial events of the past and their geological significance', *Izv. AN SSSR: ser. geolog (Moscow)* no. 7, pp. 35–53.
- Chumakov, N. M. 1993a, 'The problems of palaeoclimate in researches on evolution of the biosphere', in *Problemy doantropogennoi Evolyutsii Biosfery* (The Problems of Preanthropogenic Evolution of the Biosphere), Nauka, Moscow, pp. 106–122.
- Hooker, J. J. 1992, 'An additional record of a placental mammal (Order Astrapotheria) from the Eocene of West Antarctica', *Antarctic Sci.* vol. 4 no. 1, pp. 107–108.
- Kalandadze, N. N. & Rautian, A. S. 1980, 'About the historical zoogeography of paleozoic and the beginning of Mesozoic', in *Paleontologiya. Stratigrafia (Palaeontology: Stratigraphy)*, Nikko, Moscow, pp. 93–102.
- Kalandadze, N. N. & Rautian, A. S. 1981, 'The intercontinental connections of terrestrial tetrapods and resolution of the problem of Scotch fauna Elgin', in *Zhizn' na drevnikh kontinentakh, ee stanovlenie i razvitiye* (The Life on ancient continents, its formation and development), Proc. 23 sessions of All-Union Palaeont. Soc., Nikko, Leningrad, pp. 124–133.
- Kalandadze, N. N. & Rautian, A. S. 1983, 'The place of Central Asia in zoogeographical history of the Mesozoic', in *Iskopaemye reptilii Mongolii. Trudy Sovm. Sov. Mong. Palaeont. Ekspeditsii* (Fossil Reptiles of Mongolia), Proc. Common Sov. Mong. Palaeont. Expedition, Nikko, Moscow vol. 24, pp. 6–44.
- Kalandadze, N. N. & Rautian, A. S. 1991, 'Late Triassic zoogeography and a reconstruction of the terrestrial tetrapod fauna of North Africa', *Paleontol. Journ.*, vol. 25 no. 1, pp. 1–12.
- Kalandadze, N. N. & Rautian, A. S. 1992, 'The system of mammals and historical zoogeography', in *Filogenetika mlekopitayushchikh* (Phylogeny of mammals), Proc. of Zoological Museum, MSU, vol. 29, Moscow State University, Moscow, pp. 44–152.
- Kalandadze, N. N. & Rautian, A. S. 1993a, 'The Jurassic ecological crisis of community of terrestrial tetrapods and heuristic model of conjugate evolution of community and its biota', in *Problemy doantropogennoi evolyutsii biosfery* (The problems of preanthropogenic evolution of the biosphere), Nikko, Moscow, pp. 73–91.
- Kalandadze, N. N. & Rautian, A. S. 1993b, 'Symptoms of ecological crises', *Stratigraphy and Geological Correlation*, vol. 1 no. 5, pp. 473–478.
- Kalandadze, N. N. & Rautian, A. S. 1995 (in press), 'Physiological precondition of mastering of vegetative resources by terrestrial vertebrates', *Paleontolog. Zh.*
- Lyubishchev, A. A. 1982, *Problemy formy, sistematiiki i evolyutsii organizmov* (The Problem of form, Systematics and Evolution of Organisms), Nikko, Moscow, 278 pp.
- Olson, E. 1966, 'Community evolution and the origin of mammals', *Ecology*, vol. 47 no. 2, pp. 291–302.
- Rasnitsyn, A. P. 1988, *Phylogenetics. Sovremennaya paleontologia* (Modern Palaeontology), Nedra, Moscow, pp. 480–497.
- Rautian, A. S. 1990, *A heuristic model of formation of homoiothermy. X Vses. soveshchi, po evolyutsionnoi fiziologii* (All-Union Conf. on evolutionary physiology), Nikko, Leningrad, pp. 31–32.
- Skarlato O. A. & Starobogatov, Ya. I. 1974, 'Phylogenetics and the principles of construction of natural system', in *Teoreticheskie voprosy sistematiiki i filogenii zhivotnykh* (Theoretical questions of systematics and phylogeny of animals), *Science*, C, pp. 30–46.
- Wallas, A. R. 1876, *Die geographische Verbreitung der Thiere*, R. v. Zahn Verl, Dresden, Bd 1, p. 578 S; Bd 2, p. 258.

## 4.4 Biogeography and Evolution of Faunistic Complexes

E. B. Naimark and A. V. Markov

### Introduction

The distribution of taxa and/or regional faunistic complexes are usually considered to be the subject of biogeography. Biogeographical studies involve both the study of the geographic spread of a taxon as well as the composition of a faunal complex (Beklemishev 1982). Those who study the first area generally construct maps, while the others prefer to construct fauna lists. When carrying out such studies one must take into account the uncertainty of the paleogeographical reconstructions used and the fact that paleontological data are not continuous either in space or in time. When incomplete data are plotted against the uncertain map, the reliability of the final conclusions appears to be doubtful.

One needs to also consider that paleontologists usually study a whole sequence of biogeographical schemes changing through time, not just a single momentary biogeographical portrait. The time aspect makes it necessary to take into account the evolution of the taxa. In a comparative analysis of the dynamics of the biogeographical structure during the development of different regional complexes one needs to distinguish extrinsic and intrinsic sources of the biogeographical variability, to estimate the influence of the extrinsic factors on the system during the crisis epochs and to evaluate the possibilities of forecasting the system's behaviour. This paper represents the results of the study of the evolution of spatial structure and other characteristics of some regional taxonomic complexes.

### Integrity and evolution of regional faunas

The analysis of the development of regional taxonomic complexes, namely the changes in composition and proportion of different taxa, is an important part of distinguishing biogeographical provinces.

A complicated and little-studied aspect of this kind of research is the concept of the minimal faunistic complex and the difference between ecological and biogeographical elements (see detailed discussion in: Levushkin 1975; Starobogatov 1970, 1982; Semenov 1982). As for paleontologists, the study of several sample assemblages seems the most useful approach (Rosen & Smith 1988). Without going into details, we can only point out that the determination of a minimal faunistic complex (minimal unit of biogeographic study) is also very practical for stratigraphical purposes, because it is connected directly with the problem of estimating the possibilities of the correlation of the zonal stratigraphical scales.

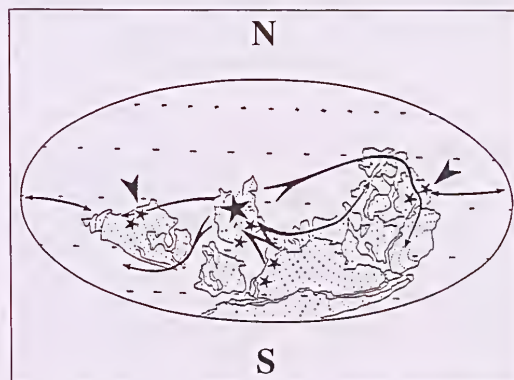
In the present chapter we shall attempt to demonstrate that regional complexes of quite different sample size

reveal similar characteristics and show one and the same general sort of development.

One of the typical examples is the development of the regional faunas of regular archaeocyathians in the Early Cambrian (Naimark & Rozanov, in press). Eleven equatorial and subequatorial shelf basins have been regarded as regional complexes: the Siberian Platform, the Altay–Sayan Fold Belt, Mongolia, the Far East, Kazakhstan, China, North Africa, Western Europe, Australia, Western and Eastern parts of North America. This division is artificial to some extent, but it is convenient and sufficiently substantiated by the experience of archaeocyathian researchers over the last two decades (Debrenne et al. 1990).

In nine regions the first recorded faunas contain primitive, unspecialized genera: *Archaeolynthus*, *Dokidocyathus*, *Ajacicyathus*, *Nochorocyathus*, *Erismacoscinius* amongst others. All these genera originally appeared in Tommotian rocks of the Siberian Platform. Later, they spread into the other ten regions. The Siberian Platform served as a centre of origin for many Early Cambrian taxa (fig. 1; Rozanov 1992).

After the initial stage of regional fauna origins, the next phase was marked by the development of more specialized forms. Generalists gradually gave way to specialists. The process of specialization of forms in the regional faunas may result from immigration or local origin. Specialized immigrants originated in the secondary centres of diversification: the Altay–Sayan fold belt, North Africa and Australia. This second phase of regional fauna development is marked by a time of maximum faunal diversity and the maximum tempo of origin of the endemic genera. During this phase rapid



**Figure 1** Scheme of distribution of the Early Cambrian taxa. Stars indicate the centers of diversification; large star shows the center of origin on the Siberian platform (from Rozanov 1992)



emigration from the secondary centres of diversification occurred (table 1). Origination of endemic genera and immigration of short-lived taxa is apparently related to the increase of ecological specialization in each regional fauna. The ecological specialization increases the probability of extinction (Cope 1896; Depere 1915; Sepkoski 1992; Markov & Naimark 1994). Slight environmental fluctuations can be enough to bring about extinction of a stenoeic (ecologically specialized) form, while an euryoeic (ecologically not specialized) form requires greater fluctuations to bring about extinction. At the Mesozoic–Cenozoic boundary the echinoid order Holasteroida suffered much greater extinction on the species and generic levels than the closely related order

Spatangoida. These two orders, though very similar in morphology and ecology, had one important difference: holasteroid genera and species by the end of the Cretaceous were, on average, decidedly more specialized than spatangoid taxa of the same rank (Markov & Solovjev, this volume).

The rule of selective extinction of specialized forms is correct not only for the taxon as a whole, but also for the regional taxonomic complex. With regard to regular archaeocyathians, by the beginning of the Botomian regional complexes were characterized by a high percentage of specialized genera. By the middle of the Botomian, a considerable decrease of diversity occurred.

Siberia

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	4	4	0	0
b3	0	0	0	0
b2	12	0	0	0
b1	54	1	8	8
at4	40	4	6	8
at3	28	1	2	2
at2	26	0	1	2
at1	24	0	0	13
t	12	0	2	12

Altai–Sajan fold belt

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	4	0	0	0
b3	40	0	0	0
b2	84	1	4	5
b1	90	2	10	13
at4	71	3	3	7
at3	55	5	6	17
at2	27	15	2	9

Mongolia

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	4	0	0	0
b3	28	1	0	0
b2	61	0	1	1
b1	72	18	6	6
at4	43	13	1	1
at3	24	12	1	1
at2	8	6	0	0

Far East

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	2	0	0	0
b3	26	1	1	1
b2	47	7	1	1
b1	44	16	1	1
at4	27	5	0	1
at3	20	10	0	0
at2	10	3	0	0
at1	6	5	0	1

North Africa

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	0	0	0	0
b3	11	0	0	0
b2	28	2	2	2
b1	24	6	2	2
at4	16	2	0	0
at3	16	3	0	1
at2	9	4	1	5

Far East

age	total number of genera	number of immigrants	number of endemics	number of emigrants
tn	2	0	0	1
b3	46	0	0	0
b2	63	3	10	10
b1	56	11	22	23
at4	13	10	1	2
at3	1	1	0	0

Table 1 Renovation of the regional faunas of regular archaeocyathes (Regulares)



mostly due to the extinction of specialized genera. After this extinction, regional faunas became more cosmopolitan: each fauna contained only a few euryoecic, widely distributed genera.

At the end of the Botomian, the last of the ancient euryoecic genera, which had originated in the primary centre of diversification, became extinct. During the Toyonian, regional faunas contained only a few genera which had originated during the Botomian.

Analysis of the development of regional faunas in regular archaeocyathians helped to reveal the following:

1. Regional complexes of the archaeocyathians possessed an integrity caused by ecological interactions of the closely related genera;
2. Development of the regional complex apparently was determined not only by the local environmental conditions, but also by the mechanisms that regulated the structure of the regional complex, the ratio of generalists and specialists. The similarity of these mechanisms was probably the reason for the similar pattern of development in all eleven regional complexes of archaeocyathians;
3. Mass origination of endemic genera occurred during the period of the greatest taxonomic diversity. There are no actual reasons to suggest that this event was caused by the increase of geographical isolation. More precisely, when the regional faunas are in their acme, any difference in abiotic or biotic conditions may serve as a geographical barrier. This is suggested by analysis of the ratio of *de novo* endemics and immigrants. Periods of maximum tempo of origination of endemic genera and the periods of maximum immigration coincide in time (table 1). Moreover, during the acme phase, regional faunas become increasingly more different from one another. This period can stimulate the origination of the endemic forms;
4. The decrease of the biogeographical differentiation in Archaeocyatha at the end of the Botomian may have been caused not only by the disappearance of the physical barriers, but also by the extinction of many of the specialized genera with restricted geographical distributions.

The studies of the development of smaller faunistic complexes (different Cambrian seas on the North American continent) led to the concept of biomes in stratigraphic sequences (Palmer 1965, 1979; Stitt 1971, etc.). Biomes are regional stratigraphic intervals containing one taxonomic complex. The different phases of a biome are the same as in the regional complexes of archaeocyathians described above. First, the long-lived generalists appear, then the short-lived forms; there are many endemics among the latter. The extinction of the

specialists is followed by the extinction of the pioneer euryoecic forms. The last phase, which is not a part of archaeocyathian faunal history, is development of marginal complexes of short-lived species. Apparently, the succession of events in the biome is controlled by the same intrinsic mechanisms as those controlling large regional complexes.

The parallelism in the development of regional faunas and similarity in the patterns of extinction and origination have been noted by Oliver and Pedder in their research on regional faunas of rugose corals (Oliver & Pedder 1994). These authors revealed similarity in the development of the faunas of both large and small regions. They came to the conclusion that the development of coral fauna was controlled by some general mechanisms that did not depend upon the geographical position of the particular region.

We can see that integrity and historical development are characteristics of faunistic complexes of quite different size, from those of small seas to others inhabiting vast shelf basins.

#### Interaction between the elements of a biogeographical system

Any system is characterized by its elements and the ways they interact. Section 2 of this paper dealt with the elements of the system (a global fauna is considered to be a system; regional faunas make up its elements). In this section we discuss characteristics of interaction of these regional complexes. The connections between the regional complexes are mostly due to the euryoecic forms capable of spreading. Such forms are usually tolerant of the environmental differences between the sea basins. The regional individuality is maintained by the endemic, short-lived forms. The euryoecic forms can be used to distinguish the centres of diversifications (regions of mass origination of euryoecic, tolerant genera and species). Several features of the centres of diversification have been revealed in the analysis of the distribution of Paleozoic bryozoan genera (Markov et al., in press). Bryozoan taxonomy by Gorjunova (1992) was used.

We have studied the tempo of origination of new bryozoan genera and their total abundance in the following regions: Eastern Europe, Western Europe and North Africa, Urals, China, North-East Asia (Siberia, Mongolia, Altay–Sayan Fold Belt), Australia, North America, Kazakhstan. Tempo of origination was estimated by means of the total generic geographical distribution index (integral area inhabited by the new genera was calculated instead of number of genera; this makes it possible to take into account not only the quantity, but also the quality of the new genera; for more detail see: Gorjunova et al., this volume). We have estimated the degree of evenness of distribution of the two parameters (diversity and tempo of origination) among the regions. The coefficient of evenness of the Shannon's

index ( $I_e$ ) was used (Pielou 1969; Magurran 1983; Foot 1995):

$$I_e = \sum_{i=1}^N P_i \cdot \log_2 p_i / \sum_{i=1}^N (1/N) \cdot \log_2 (1/N),$$

where  $N$  - number of regions (8),  $P_i$  - total geographical distribution index (GDI) of genera which originated during the particular age in the particular region divided by total GDI of all genera which originated during the epoch.

Calculations demonstrated that the origination of new genera was distributed among the regions much less evenly than the generic diversity (table 2). Moreover, the 'probability unevenness' of origination appeared to be considerably lower than the real unevenness. The 'probability unevenness' was calculated by means of computer experiment: all genera known to originate in the particular age were distributed randomly among the regions, in accordance with the generic diversity in each particular region. It was shown that the suggestion, according to which the observed unevenness of origination was caused by random factors, has a probability of only 0.0012.

**Table 2**

Evenness of distribution of regional diversity and regional origination in the order Trepostomida (Bryozoa)

time $I_e$	O-a- O-ld	O-ca- r-O <sub>1</sub>	S	D <sub>1</sub>	D <sub>2</sub>	D <sub>3</sub>	C	P <sub>1</sub>	P <sub>2</sub>
$I_e$ of origination	0.48	0.30	0.38	0.45	0.45	0.48	0.64	0.27	0.46
$I_e$ of diversity	0.63	0.85	0.80	0.84	0.84	0.81	0.89	0.83	0.80

Our research demonstrates that the origination of euryoecic, long-lived genera is not directly related to diversity, although in some modern models of evolution (Sepkoski 1991) the number of originations depends directly upon the taxonomic diversity. These results also support the reliability of the paleontological data on the tempo of origination of taxa in different regions.

Analysis of the distribution of the origination of new genera in time and space shows that in each regional fauna there are periods of origination of local forms and periods of maximum diversity. But there are only a few regions in each geologic epoch, where euryoecic genera, capable of spreading, originate. It seems logical to call such regions 'centres of diversification'.

Euryoecic forms migrate from the centre of diversification into the other regions, thus changing the characteristics of the regional complex. When the first pioneer representatives of a new higher taxon appear, the percent ratio of taxonomic groups changes abruptly.

Afterwards this ratio, with some particular taxa dominating, tends to remain constant for some time (fig. 2). For example, let us consider the changes in the ratio of five suborders of trepostomid and cystoporid bryozoans in two regions: Eastern Europe and North America. The dominance of Halloporeina in the Ordovician and Silurian was followed by the dominance of Amplexoporeina in the Middle Devonian - Carboniferous. In the Middle Devonian the percentage of Hexagonellina increased in the North American fauna, but in Eastern Europe this suborder was not present until the Early Carboniferous. East European expansion of Hexagonellina in the Early Carboniferous resulted in decrease of percentage of Fistuliporeina. The new proportion of the suborders in Eastern Europe remained almost constant through the Carboniferous (fig. 2). New genera, whose origination took place in the centres of diversification, changed the taxonomic structure of the regional complex and became new ecological dominants.

In our studies we have examined the rate of origination of new genera in four Paleozoic Bryozoan orders in different regions (Markov et al. in press). This rate appears to be quite different for different orders (fig. 3) and the new genera occupied different volumes of adaptive space. Euryoecic genera developed in centres of diversification not simultaneously in all orders, but only in one or a few orders at a time. For instance, figure 3 shows that in the Early Devonian in Western Europe there was a high rate of origination of new euryoecic genera in the order Fenestellida, while in the other three bryozoan orders this rate was low. During the Middle Devonian the greatest volume of adaptive space was occupied by the new North American genera of Cystoporida and Rhabdomesida; in the order Fenestellida most euryoecic genera originated in Central Asia; North America and China were the centres of diversification of the order Trepostomida.

The rate of origination of euryoecic genera varies through time. For example, this can be observed by plotting the dynamics of origination of genera that spread into the other regions (table 3). The ability to disperse is characteristic of euryoecic genera (those with broad environmental tolerances), as mentioned before. The periods of mass origination of such genera took place in Eastern Europe during the Early Ordovician and Late Silurian; in North America, during the Middle Ordovician, Middle Devonian and Early Carboniferous; in Siberia, during the Middle Ordovician, Early Silurian, Middle Devonian, Tournaisian and Serpukhovian; in Kazakhstan, during the Famennian and Tournaisian, in Australia, during the Early Permian. The highest origination rates of such genera took place during the Early Ordovician, and immediately after the mass extinctions at the Early-Middle Devonian boundary as well as at the end of the Devonian. The extinctions produce vacant ecological space and may encourage the origination of euryoecic genera.



New euryoecic forms usually invade the region after the extinction of the formerly predominant group. For instance, the representatives of Trepostomida became abundant in Siberia and Mongolia only during the Caradocian, although they were already widely distributed in East European and North American basins earlier. The invasion of Trepostomida into Siberia has likely been delayed because of the dominance of Cryptostomida (Siberia was the centre of diversification of the latter order). Another example can be found in the distribution of the ammonite order Prolecanitida (the order rank of this group and its division into two superfamilies, Medlicottitaceae and Prolecanitaceae, was proposed by Weidmann and Kullmann, 1981). The pioneer euryoecic representatives of Medlicottitaceae originated at the end of Early Carboniferous and during the Middle Carboniferous in Eastern Europe and the Urals. The group moved into North American basins

during the Bashkirian and especially during the Late Carboniferous. Until the Serpukhovian North American seas were dominated by another superfamily, Prolecanitaceae, but in Serpukhovian and Bashkirian the diversity of North American Prolecanites was low. Probably the extinction of the local dominants (Prolecanitaceae) was a necessary factor encouraging the immigration and intensive radiation of Medlicottitaceae.

Thus, there are at least four features of the centres of diversification:

1. The rate of origination of new genera is not directly correlated with the level of diversity in the region;
2. It is the centres of diversification where the changes of ecological dominants and of the faunistic complex structure are initiated;
3. Periods of mass origination do not occur simultaneously in all taxa present in the region;
4. Centres of diversification sometimes appear during periods of crisis following the extinction of some dominant taxa.

Analysis of the characteristics of centres of diversification and study of the mechanisms of origination of euryoecic genera are two possible ways of exploring the interaction factors that control the biogeographic distribution through time. Another way is to analyze the communications of the regional complexes and the routes of migration of species and genera. It is commonly accepted that the geographical distribution and migrations of benthic forms depend upon various environmental factors, such as ocean currents. Without trying to downgrade the significance of these factors, we would like to point out that a regional faunistic complex, due to its integrity, can be capable of controlling the intensity and direction of migrations. We shall give several examples.

Genera of the Paleozoic bryozoan order Trepostomida, which originated in the centres of diversification during different epochs, replaced each other according to a strict chronological sequence in each of the eight regions studied (table 4; Naimark et al. in press). The earlier the genus originated, the earlier it spread into another region, with no relation to the epoch of migration. Genera that originated during the Devonian, never occupied any region before the Ordovician genera. Early Carboniferous genera never invaded a region before the Devonian ones, or Late Carboniferous genera before the Early Carboniferous ones. It is highly improbable that such a sequence was caused by random factors. Thus, it is more reasonable to suggest that the succession of immigration was controlled not only by extrinsic factors, such as ocean currents or distances between the basins, but also by the factors of intrinsic nature, for instance, the structure of the regional complex.

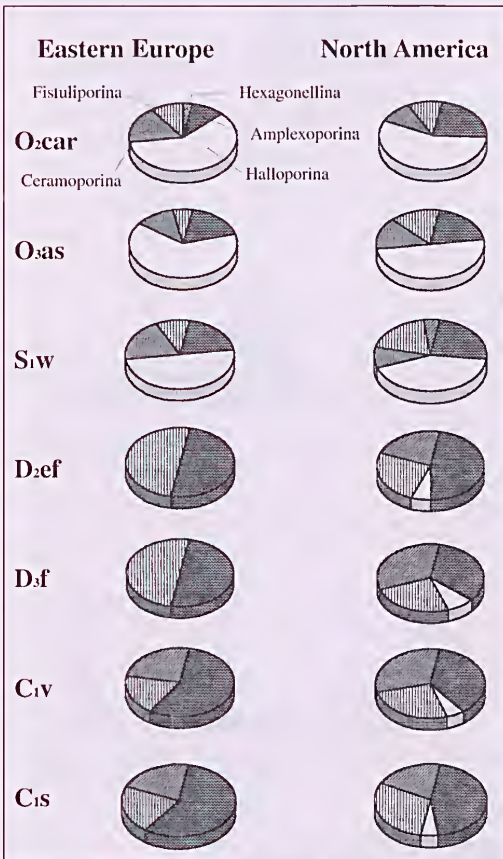


Figure 2

Changes in percentage of five Bryozoan suborders during the Paleozoic in Eastern Europe and North America. Order Trepostomida: suborders Halloporina and Amplexoporina; order Cystoporina: suborders Ceramoporina, Fistuliporina and Hexagonellina. O2car - Caradocian, O3as - Ashgillian, S1w - Wenlockian, D2ef - Eifelian, D3f - Frasnian, C1v - Visean, C1s - Serpukhovian.



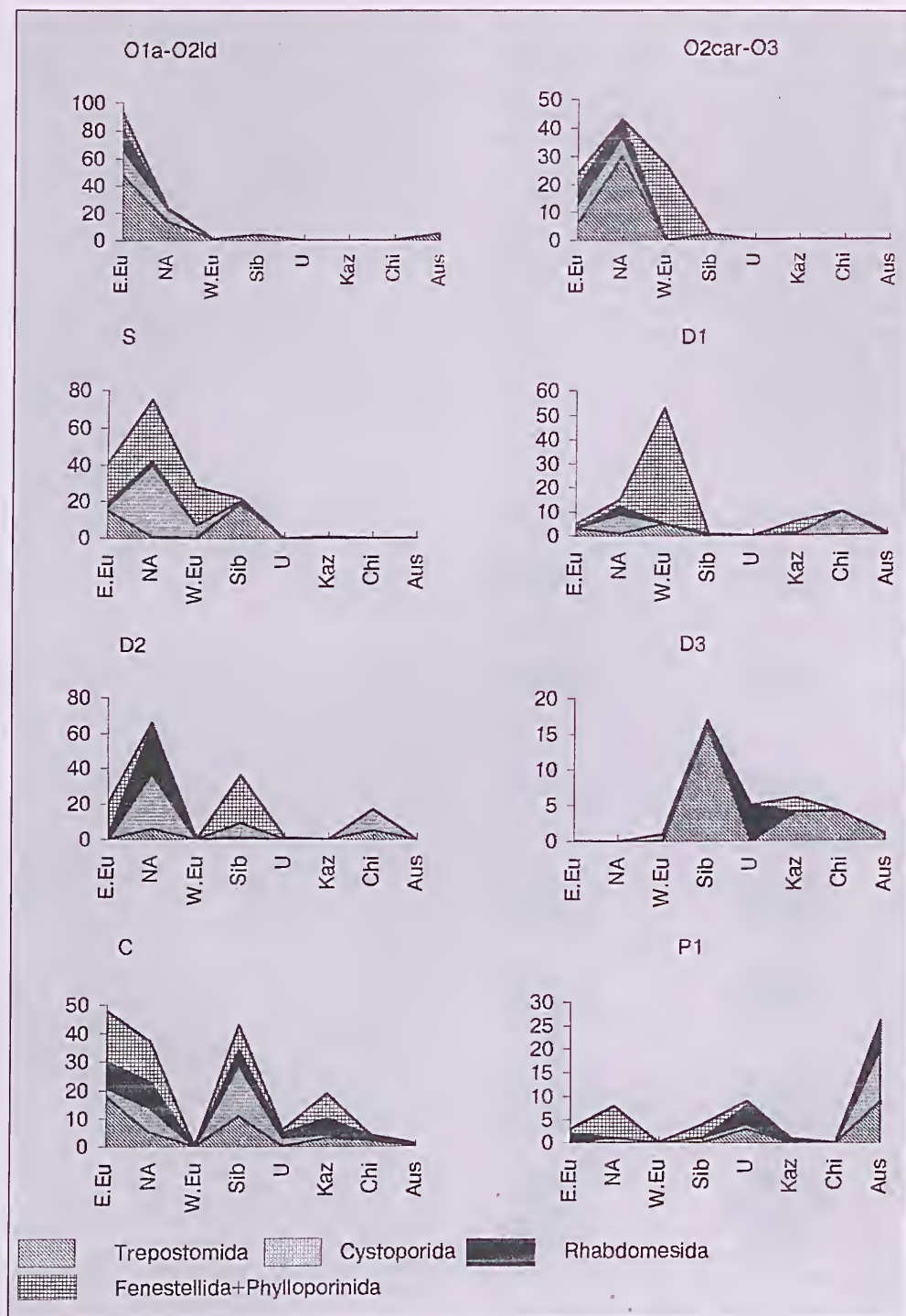


Figure 3

Tempo of origination of genera of four Bryozoan orders in the regions: E.Eu. — Eastern Europe, N.A. — North America, W.Eu. — Western Europe, Sib. — Siberia, U. — Urals, Kaz. — Kazakhstan, Chi. — China, Aus. — Australia. Regions plotted on X axis. Width of bands plotted on Y axis shows total geographical distribution index (GDI) of the new genera in one of the four orders. GDI is approximate area inhabited by a genus at the time of its maximum distribution.

Age	Eastern Europe	North America	Western Europe	Siberia + Mongolia	China	Kazakhstan	Australia
O1a	6						
O1l	6						
O2ld	10	3		5			
O2car	7	5					
O2as	1	3	1				
S2l	2	2		3			
S1w	4	3	1			1	
S2ld	1	1	1	1			
S2p	2	1					
D1l	1	2	2		1		
D1p						1	
D1e	2		1			1	
D2ef		5		2	1		
D2gv		1		3	1		
D3f				1			
D3fm						2	
C1t	2	3		6		2	
C1v	1				1		
C1s		1		3			
C2	2						
C3	1						
P1a							1
P1s				1			1
P1ar							2
P1k							

Table 3

Number of new bryozoan genera which later migrated into other regions. Time and place of origination are shown.

The study of the mollusc distribution in the North Pacific shelf during the Cenozoic has led to the conclusion that migration routes did not follow paleocurrents, but reflect movement from regional complexes of high diversity to those of low diversity (Kafanov 1982).

Our study of the distribution of rugose corals during the Devonian confirms the observation for molluscs. We have used data on generic diversity, collected by L. M.Ulitina.

In figures 4–6 the arrows indicate direction of migration of *Rugosa* in ten Devonian basins of Russia and adjacent countries. Regions with high generic diversity are marked with double lines. The figures show that genera of *Rugosa* migrated mostly from the regions with a diverse fauna. The most intensive migration usually followed periods of maximum diversity of the regional fauna. The most spectacular examples are: Urals during the Emssian and Frasnian, Yakutia and Altay–Sayan region during the Eifelian, Kazakhstan during the Pragian (the figures do not show the Lohkovian age, when the fauna of Kazakhstan was the most abundant (Ulitina & Naimark, in press)).

Thus, when analyzing the communications between regional faunas of the ocean basins, it is necessary to take into account not only environmental/geographical factors but also the characteristics of the faunistic complexes involved.

### Conclusion

The regional taxonomic complex (faunistic complex) is characterized by its integrity and historical development. These two features are integrally related to the regular succession of phases of growth, acme and decline. This sequence is determined by the internal interactions of the elements of the taxonomic complex.

Communication between the faunistic complexes is made possible by the movement of euryoecic forms, which originate in the centres of diversification.

The centres of diversification (CD) are characterized by the following features:

1. Tempo of origination in CD does not depend directly upon the diversity;

Table 4

The succession of immigration of genera of Rhabdomesida (Bryozoa). The table shows the age and place of origination of genera.

Age of immigration	Eastern Europe	North America	Siberia & Mongolia	China	Kazakhstan	South-East Asia
O-car		EE-O.ld, EE-O.ld	EE-O.ld,			
O-as		EE-O-car				
S.l			EE-O.ld EE-O-car			
S.w	NA-S.l					
S.ld						
S.p						
D.l						
D.p						
D.e						
D.ef					EE-O.ld	
D.gv		EE-D.ef		P-O-car		
D.f			NA-D.ef, NA-D.ef	NA-D.ef	NA-D.ef, NA-D.ef	
D.fm						
C.t	NA-D.ef	NA-D.ef	NA-D.ef, P-D.fm	NA-D.ef,	NA-D.ef, SM-C.t	
C.v			P-C.t,KZ- C.t			
C.s						
C.b						
C.m						
C.k	NA-D.ef,P- D.fm	SM-C.v	SM-C.v			
C.g						
P.a	NA-C.t, NA-C.t		P-C.t		NA-C.t	NA-D.ef, P- C.t, NA-C.t
P.s						
P.ar			EE-C.g			
P.k						
P.kb	U-P.k		P-P.ar	NA-C.t, P-P.a, SEA- P.ar		
P.mr						

EE — Eastern Europe, NA — North America, SM — Siberia and Mongolia, CH — China, KZ — Kazakhstan, SEA — South-East Asia, P — polyregional (genus that first appeared in more than one region during one age). P2kb — Kubergandinian. Other abbreviations: see table 3.

2. Major changes of taxonomic structure of the faunistic complex take place in CD;
3. Not all the taxa present in CD are involved in the intensive origination of new forms, only some;
4. Euryoecic forms migrate out of the CD into the other regions after the extinction of local dominants.

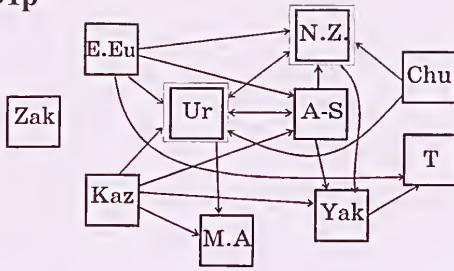
The nature of the regional complex, combined with the other factors, control the migration of taxa from one region to another.

## References

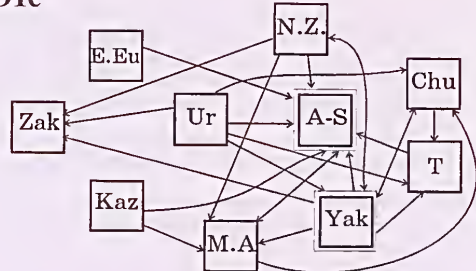
- Beklemishev, K. V. 1982, 'On the nature of biogeographic proofs', *Marine Biogeography*, Nauka, Moscow, pp. 5-11 (in Russian).
- Cope, E. D. 1896, *The primary factors of organic evolution*, Open Court Publ. Co., Chicago, 547 pp.
- Debrenne, F., Rozanov, A. Yu. & Zhuravlev, A. Yu. 1990, *Regular Archaeocyathes*, Cahiers de paléontologie, Paris, 218 pp.
- Depere, S. 1915, *Changes of the animal world*, Stasyulevich Publ., St Petersburg, 269 pp. (in Russian).
- Foot, M. 1995, 'Morphological diversification on Paleozoic crinoids', *Paleobiology*, vol. 21 no. 3, pp. 273-299.
- Gorjunova, R. V. 1992, *Morphology and systematics of Paleozoic Bryozoans*, Nauka, Moscow, 165 pp. (in Russian).
- Gorjunova, R. V., Markov, A. V. & Naimark, E. B. (this volume), 'Diversity dynamics in the order Trepostomida (Bryozoa)', *Rec. Queen Vict. Museum*, no. 104, pp. 25-29.
- Kafanov, A. I. 1982, 'Cenozoic history of malacofaunas of North Pacific shelf', *Marine biogeography*, Nauka, Moscow, 134-176 (in Russian).
- Levushkin, S. I. 1975, 'On ecological faunistic complexes (illustrated by underground faunas)', *Journal of General Biology*, vol. 36 no. 6, pp. 814-828 (in Russian).
- Levushkin, S. I. 1982, 'Problem of island faunas in the light of relations between biogeography and ecology', *Marine biogeography*, Nauka, Moscow, pp. 26-52 (in Russian).
- Magurran, A. E. 1983, *Ecological diversity and its measurement*, Croom Helm, London-Sydney, 184 pp.



**D1p**



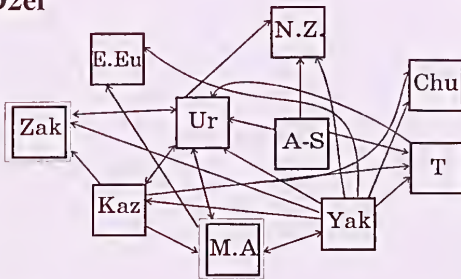
**D1e**



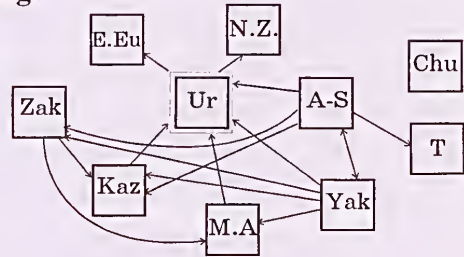
**Figure 4**

Scheme of migration of Rugosan genera during the Pragian and Emsian ages in ten regions of Russia and adjacent regions. Regions are shown as rectangles; regions with high level of diversity are marked with double border. Regions: E.Eu. — Eastern Europe, Zak. — Zakavkazye, Kaz. — Kazakhstan, Ur. — Urals, N.Z. — Novaya Zemlya, A. — S. — Altay — Sayan region, Chu. — Chukotka, T. — Taymyr, Yak. — Yakutia, M.A. — Middle Asia, D1p — Pragian, D1e — Emsian.

**D2ef**



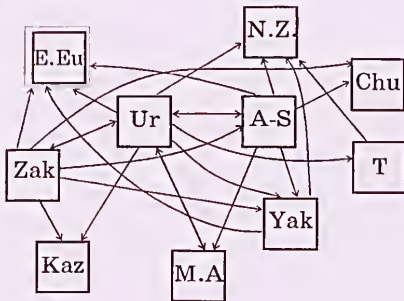
**D2gv**



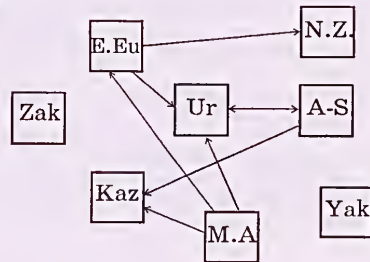
**Figure 5**

Migration of Rugosan genera in 10 regions during the Middle Devonian. D2ef — Eifelian, D2gv — Givetian. Symbols and abbreviations same as in figure 4.

**D3f**



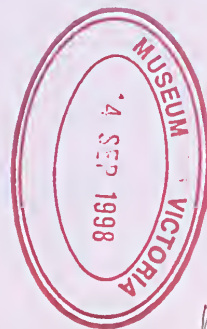
**D3fm**



**Figure 6**

Migration of Rugosan genera in 10 regions during the Late Devonian. D3f — Frasnian, D3fm — Famennian. Symbols and abbreviations same as in figure 4.

- Markov, A. V. & Naimark, E. B. 1994, 'Selective extinction of specialized taxa and its role in the evolution of biota', *Journal of General Biology*, vol. 55 no. 6, pp. 673–683 (in Russian).
- Markov, A. V., Naimark, E. B. & Gorjunova, R. V. (in press), 'Some biogeographic regularities of origination and the problem of centres of diversification (illustrated by Paleozoic Bryozoans)', *Journal of General Biology* (in Russian).
- Markov, A. V., E. B. & Solovjev, A. N. (this volume), 'Echinoids at the Cretaceous–Paleogene boundary', *Rec. Queen Vict. Museum*, no. 104, pp. 35–37.
- Naimark, E. B., Markov, A. V. & Gorjunova, R. V. (in press), 'Dynamics of regional diversity of Paleozoic Bryozoans of the order Rhabdomesida', *Paleont. Journal*.
- Naimark, E. B. & Rozanov, A. Yu. (in press), 'Regularities of development of regional faunas of Regular Archaeocyathes (class Regulares)', *Stratigraphy: Geological correlation*.
- Oliver, W. A. & Pedder, A. E. H. 1994, 'Crises in the Devonian history of the rugose corals', *Paleobiology*, vol. 20 no. 2, pp. 178–190.
- Palmer, A. R. 1965, 'Biomere — a new kind of biostratigraphic unit', *Jour. Paleontology*, vol. 39, pp. 149–153.
- Palmer, A. R. 1979, 'Biome boundaries re-examined', *Alcheringa*, vol. 33, pp. 33–41.
- Pielou, E. C. 1969, *An introduction to mathematical ecology*, Wiley, New York, 126 pp.
- Rozanov, A. Yu. 1992, 'Some problems concerning the Precambrian–Cambrian transition and the Cambrian faunal radiation', *Jour. Geol. Soc. London*, vol. 149, pp. 593–598.
- Rosen, B. R. & Smith, A. B. 1988, 'Tectonics from fossils? Analysis of reef-coral and sea urchin distributions from late Cretaceous to Recent, using a new method', in *Gomfana and Tethys*, eds M. G. Audley-Charles & A. Hallam, *Geol. Soc. Spec. Publ.*, no. 37, pp. 275–306.
- Semenov, V. N. 1982, 'Biogeographic schemes of South American sea shelf based on classification of species areas of benthic invertebrates', *Marine biogeography*, Nauka, Moscow, pp. 184–269 (in Russian).
- Sepkoski, J. J. 1991, 'Population biology models in macroevolution', in *Analytical paleobiology*, eds Gilinsky, N. L. & Signor, P. W., *Short courses in paleontology*, no. 4. Paleontol. Society, Knoxville, T. N., pp. 136–156.
- Sepkoski, J. J. 1992, 'Phylogenetic and ecological patterns in the Phanerozoic history of marine biodiversity', in *Systematics, Ecology, and the Biodiversity Crisis*, ed. N. Eldredge, Columbia University Press, New York, pp. 77–100.
- Starobogatov, Ya. I. 1970, *Molluscs fauna and zoogeographic schemes of continental basins*, Nauka, Leningrad, 372 pp. (in Russian).
- Starobogatov, Ya. I. 1982, 'Problem of minimal sample in biogeography and its applications in faunistic (faunogenetic) marine zoogeography', *Marine biogeography*, Nauka, Moscow, pp. 12–18 (in Russian).
- Stitt, J. H. 1971, 'Late Cambrian trilobite biomes', *Jour. Paleontology*, vol. 45 no. 2, pp. 178–182.
- Ulitina, L. M. & Naimark, E. B. (in press), 'Analysis of diversity of Rugosa of Russia and adjacent countries', *Paleontol. Jour.*
- Weidmann, J. & Kullmann, J. 1981, *Ammonoid Sutures in ontogeny and phylogeny. The Ammonoidea*, Systematic Association Spec. Vol. 18, Acad. Press, New York, pp. 215–255.



MC 317